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Fungus Consumption (Mycophagy) by Small Animals

Abstract

A review of the natural history literature of small mammal feeding habits, based on many fortuitous field observations, some analysis of stomach contents, and a few feeding experiments, shows that diverse animals feed on similarly diverse fungi. The interdependence of animals and fungi has evolved to a high degree in some cases, e.g., the loss of alternative spore dispersal mechanisms by some fungi and the strong reliance of some mammals on fungi as a primary food. Consequently, adaptation for mycophagy and the effects on mycophagy of habitat, fungal toxicity, and the food value of fungi have implications in the interpretation of ecosystem structure and function.

Introduction

Truffles and other hypogeous fungi occupy a highly specialized, protected niche as subterranean-fruiting symbionts with roots of higher plants. Such fungi depend on mammal and invertebrate mycophagy for spore dispersal. These and other fungi, in turn, are important in the diet of many animals and in some cases comprise the major food source.

These interrelationships between fungi and animals engender many questions relevant to the life histories and ecosystematic roles of both. For example, which animals depend largely on fungi for food, for water, or for vitamins? What are the behavioral implications of seeking, drying, and caching fungi? What food values do mycophagists derive from fungi? Can animals differentiate between poisonous and nonpoisonous fungi? What is the phylogenetic significance of the various fungal mechanisms evolved for attracting mycophagists? What role does mycophagy play in fungus dispersal? What impact does mycophagy have on food chain and ecosystem dynamics, and where need it be recognized in ecosystem modeling?

The following literature review is intended to aid and stimulate a search for answers to such questions with emphasis on mammals, although similar questions can be asked about other animals as well. Little comprehensive research has been done on animal mycophagy. To interpret scattered fragments of published information, we have filled some gaps with speculation in hope of fostering further research in this fascinating field. Our literature search led to compilation of the reciprocal lists of mammal mycophagists and fungi eaten, presented later in this paper. Authorities for all species mentioned in the text are given in these lists.

The Small Mammal as Mycophagist

Many fortuitous field observations, some analyses of mammal stomach contents, and

a few feeding experiments have revealed that diverse mammals feed on similarly diverse fungi. The mammals include insectivores, omnivores, herbivores, and carnivores. The fungi include saprophytes, symbionts, and parasites. The interdependence of animals and fungi has evolved to a high degree in some cases, e.g., the loss of alternative spore dispersal mechanisms by the phylogenetically advanced truffles and other subterranean-fruiting fungi (Bessey, 1935; Burnett, 1968; Christenson, 1951; Kavaler, 1965; Gäumann and Dodge, 1928; Ingold, 1953, 1961, 1966; Korf, 1973; Lilly and Burnett, 1951; Rolfe and Rolfe, 1925; Smith, 1938; Trappe, 1971) and the strong reliance of some mammals on fungi as a primary food.

The Sciuridae (chipmunks and squirrels) have been the most observed mammalian mycophagists; consequently, they are also reported to eat the greatest variety of fungi. *Tamiasciurus hudsonicus* (red squirrel) has been credited with eating 89 species of fungi, more than any other mycophagist. Other relatively small mycophagists include members of the Cricetidae (mice, rats, lemmings, voles), Zapodidae (jumping mice), Ochotonidae (pikas), Soricidae (shrews), Didelphidae (opossums), Peramelidae (bandicoots), Phascolomidae (wombats), Macropodidae (rat-kangaroos), Cynopithecinae (baboons), Dasypodidae (armadillos), Leporidae (rabbits and hares), Castoridae (beavers), and Mustelidae (weasels). The reports of fungi in stomachs of shrews may at least in part reflect predation on fungus-feeding invertebrates or other animals rather than mycophagy by the shrews themselves.

The relative importance of fungi in small mammal diets has been estimated as percent of yearly dietary volume for several species (Table 1).

TABLE 1. Yearly dietary volume of fungi (%) for nine small mammal species.

Species	Volume (%)	Source
Eutamias townsendii	72	Tevis, 1953
Eutamias quadrimaculatus	66	Tevis, 1953
Spermophilus lateralis	61	Tevis, 1953
Tamiasciurus douglasii	56	McKeever, 1964
Sciurus griseus	52	Steinecker and Browning, 1970
Eutamias speciosus	32	Tevis, 1953
Eutamias amoenus	27	Tevis, 1953
Clethrionomys glareolus	7	Drożdż, 1966
Apodemus flavicollis	1	Drożdż, 1966

Tevis (1953) suggested a direct correlation between mammal body weight and importance of fungi in the diet among the *Spermophilus* spp. and *Eutamias* spp. that he studied. Other factors of habit and habitat are undoubtedly as much or more causally related to mycophagy. However, a relationship between mammal size and size of fungus eaten does seem likely in the sense that very small fungal species appear to be eaten only by smaller mammals. For instance, sporocarps of many species of the phycomycetous family, Endogonaceae, are often less than a millimeter in diameter and rarely exceed a few millimeters. These species have been reported only in stomach contents of small mammals such as shrews, voles, mice, jumping mice, pikas, etc., but they eat larger fungi as well (Bakerspiegel, 1958; Calhoun, 1941; Hamilton, 1941a; Jameson, 1952; Whitaker, 1962, 1963a; Whitaker and Ferraro, 1963; Whitaker and Maser, 1976).

Adaptations for Mycophagy

Morphological adaptations of small mammals are probably directly related to mycophagy. Animals adapted for digging might be expected to have an advantage in the search for truffles and other hypogeous fungi. Species with weak teeth might be more impelled to eat fungi when available. Unfortunately, the data presently available are too scanty to test these hypotheses.

Mammalian food-gathering behavior has evolved for locating fungi. Tevis (1953) observed innumerable small pits left in the soil from extraction of hypogeous fungi by animals; indeed, mycologists have long used this sign to indicate when and where to seek such fungi. Small mammal mycophagists probably locate hypogeous fungi by odor. Most hypogeous fungi have a noticeable odor at maturity which is almost overwhelming to many humans (Parks, 1919). Often the presence of these fungi is not visible on the soil surface. The ability of squirrels to detect mast by odor has been reported many times (Allen, 1943; Cahalane, 1942; Cram, 1924; Dice, 1927; Ingles, 1947; Ognev, 1940). We have observed over years of extensive collecting of hypogeous fungi that sporocarp odor is not detectable on immature specimens. As some spores reach maturity, a light odor often can be noticed; as the proportion of mature spores increases, so does the intensity of odor. Thus the fungus may remain undetected at early stages of development but emits increasingly strong odors as it matures.

Bright color as well as odor may attract small mammals to epigeous mushrooms and puffballs (Ingles, 1947). Mushrooms are sometimes nibbled *in situ* but are also harvested whole. Numerous observers have reported mushrooms hung in tree branch forks by squirrels, at times the tree "appearing bedecked for Christmas," (Cram, 1924; Hatt, 1929; Krieger, 1967; Marie, 1927, Odell, 1925, 1926; Ognev, 1940; Stakhrovskii, 1932). Since dried fungi preserve indefinitely, the intent of the squirrels is presumably to dry them for caching. Hardy (1949) found a cache of sporocarps left by a *Tamiasciurus hudsonicus* in a hollow tree trunk.

Mycophagy and Habitat

The characteristics of plant communities to which small mammals have become adapted are decidedly related to mycophagy. Forests of ectomycorrhizal trees such as the Pinaceae, Fagaceae, or Betulaceae produce a greater abundance of relatively large, fleshy mushrooms and hypogeous fungi, the typical fruiting forms of ectomycorrhizal fungi (Trappe, 1962). Plant communities of vesicular-arbuscular (VA) mycorrhizal hosts such as the Cupressaceae, Aceraceae, or herbaceous plants of fields, meadows, and bogs form mycorrhizae with certain genera of the Endogonaceae, which fruit hypogeously as single spores or very small, compact sporocarps (Gerdemann and Trappe, 1974). Thus, adjacent habitat types may differ strikingly in form and biomass of sporocarps produced. The small mammals that inhabit ectomycorrhizal forests might be expected to feed more on macrofungi than inhabitants of VA-mycorrhizal meadows. Although adequate data are not available, it can be hypothesized that mycophagy in VA-mycorrhizal redwood or maple forests resembles that of meadows more closely than that of ectomycorrhizal pine or oak forests. If this hypothesis is true, the qualitative and quantitative relationships of small mammal populations between these various kinds of habitats might deserve a new look.

Estimated annual production of epigeous mushrooms is summarized for several forest types in Table 2. The data of Richardson (1970) provide the best of the estimates presented, because his estimates are based on nearly weekly visits to the study site over a period of five years. The other estimates are based on relatively scanty data.

TABLE 2. Estimated production of epigeous mushrooms per ha yr^{-1}.

Forest Type	Kg Dry Wt	Kilocalories	Source
Oak and Beech, Hungary	7-160	30,000-658,000*	Hering, 1966
Beech, near Vienna	18-170	77,400-731,000*	Hering, 1966
Beech, Poland	4-5	17,200-21,500	Drożdż, 1965
Oak on slate soil, England	12-95	53,600-407,600	Hering, 1966
Oak on limestone soil, England	3-37	12,900-158,700	Hering, 1966
Conifer, Scotland	16-30	68,600-128,700	Richardson, 1970
Conifer, xeric inland forest, Pacific Northwest, U.S.A.	3	11,200	Smith, C., 1965
Conifer, xeric inland forest, Pacific Northwest, U.S.A.	10-17*	41,200-115,800*	Cooke, 1955
Conifer, Finland	5-19	22,300-82,800	Richardson, 1970
Conifer, Sweden	180	772,200	Richardson, 1970

* Our calculation, assuming 6.4% dry wt and 4300 calories g^{-1} dry wt (cf. Table 3).

Many variables interact to account for the wide range of production estimates; two most obvious are temperature and moisture and their interaction (Smith, 1949). Consequently, each climatic region has a characteristic fruiting pattern (Bohus, 1973; Ceruti, Montacchini and Duployez, 1967; Endo, 1973; Fogel, 1976; Grainger, 1946; Wilkins and Harris, 1946). Production will vary from year to year within a region, depending on weather. Habitats within a region will vary one from another in production, depending on soils, microclimate, and vegetation.

No biomass production studies of VA-mycorrhizal fungi have been reported. However, Kessler and Blank (1972) estimated that nearly 7 million minute sporocarps of Endogonaceae occurred per ha in soil of a Michigan forest dominated by the VA-mycorrhizal *Acer saccharum* Marsh. A substantial biomass may be inferred. Fogel (1976) estimated the production of hypogeous basidiomycete and ascomycete sporocarps in a Western Oregon Douglas-fir stand to range from 11,052 to 16,753 sporocarps ha^{-1} and 2.3 to 5.4 kg dry weight ha^{-1}.

The Food Value of Fungi

Fresh, fleshy fungi range from 70 to 94 percent water by weight; large volumes therefore must be eaten to provide adequate protein and phosphorus (Miller and Halls, 1969; Winton and Winton, 1935). The drying of mushrooms by squirrels concentrates their food value. At the same time, fresh fungi might be an important source of water for animals unable to exist on bound or metabolic water when free water is unavailable (Getz, 1968; C. Smith, 1965).

Some measures of the food value of fungi are compared with those of other food sources in Tables 3-5. The data should be interpreted only in a broad sense, since several sources and differing analytical methodologies are represented in the compilation. Fresh, fleshy fungi resemble fruits and vegetables in containing substantially fewer

calories gm^{-1} than fresh nut kernels, eggs, or meat (Table 3). On a dry-weight basis, fungi compare favorably with blueberries and mast but contain about a third fewer calories than conifer seed (Table 4). Compared to nut kernels, dried mushrooms are good sources of protein, carbohydrates, and minerals but not fats (Table 5).

The net caloric value of any food to a consumer is the total caloric content digested minus the calories expended in seeking, extracting, ingesting, digesting, and excreting

TABLE 3. Caloric value of fresh foods (kcal. gm^{-1} fresh wt.).

Food	Calories	Source
FUNGI		
Agaricus bisporus	0.3-0.5	Singer, 1951; Pilát and Ŭsak, 1958
Boletus sp.	0.3	Singer, 1951
Boletus edulis	0.3-0.7	Pilát and Ŭsak, 1958; Andreotti and Casoli, 1968
Lentinus edodes	0.3	Singer, 1951
Lactarius deliciosus	0.5	Singer, 1951; Pilát and Ŭsak, 1958
Tuber melanosporum	0.4-0.6	Andreotti and Casoli, 1968
"mushrooms"	0.1-0.5	Singer, 1951; Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
Mean	0.4	
NUTS		
pine kernels	6.3	Hodgman *et al.*, 1959
Beechnut kernels	6.3-7.0	Proudfit and Robinson, 1961
butternut kernels	7.1-7.4	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
chestnut kernels	7.5-7.6	Proudfit and Robinson, 1961
hazelnut kernels	6.7	Proudfit and Robinson, 1961
hickory nut kernels	1.9	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
pecan kernels	6.6	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
walnut kernels	6.7-7.0	Proudfit and Robinson, 1961
Mean	6.2	
FRUITS		
apples	0.6	Proudfit and Robinson, 1961
blackberries	0.6	Proudfit and Robinson, 1961
blueberries	0.7	Proudfit and Robinson, 1961
cherries	0.7	Proudfit and Robinson, 1961
currants	0.6	Proudfit and Robinson, 1961
plums	0.6	Proudfit and Robinson, 1961
strawberries	0.4	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
Mean	0.6	
VEGETABLES		
lettuce	0.2	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
onions	0.5	Proudfit and Robinson, 1961
water cress	0.2	Proudfit and Robinson, 1961
Mean	0.3	
EGGS and MEAT		
eggs	2.5	Proudfit and Robinson, 1961
beef	1.8-3.4	Hodgman *et al.*, 1959; Proudfit and Robinson, 1961
Mean	2.1	

the nondigested residual of that food. The relative value of fungal caloric sources for any mycophagist must be compared to other sources in terms of an energy budget. If less energy is expended per calorie gained in seeking and eating fungi than in seeds or insects, the relative value of fungi as an energy source is increased.

TABLE 4. Caloric value of dried plant parts (kcal. gm^{-1} dry wt.).

Food	Calories	Source
FUNGI		
Peridermium harknessii		
in *P. contorta* bark	5.0	Smith, C. 1965
Rhizopogon sp.	4.9	Smith, C. 1965
Russula decolorans		
gills and spores	4.8	Smith, C. 1965
pileal context	4.0	
stipe	4.2	
Suillus tomentosus		Smith, C. 1965
tubes and spores	5.2	
pileal context	4.2	
stipe	4.1	
Mean	4.5	
CONIFER SEEDS		
Abies amabilis	6.8	Smith, C. 1965
Abies lasiocarpa	7.1	Smith, C. 1965
Picea engelmanii	7.1	Smith, C. 1965
Picea excelsa	6.7	Danilov, 1938
Pinus contorta	6.8	Smith, C. 1965
Pinus silvestris	6.2	Danilov, 1938
Pinus monticola	7.4	Smith, C. 1965
Pinus ponderosa	7.6	Smith, C. 1965
Pinus pumila	6.9	Danilov, 1938
Pseudotsuga menziesii	7.1	Smith, C. 1965
Tsuga heterophylla	7.1	Smith, C. 1965
Mean	7.0	
MAST		
Acer saccharinum	4.2	Smith, C., 1970
Carya ovata	7.2	Smith, C., 1970
Juglans nigra	6.3	Smith, C., 1970
Quercus alba	4.0	Smith, C., 1970
Quercus macrocarpa	4.2	Smith, C., 1970
Quercus shumardii	5.3	Smith, C., 1970
Mean	5.2	
FRUIT		
Vaccinium deliciosum	5.3	Smith, C. 1965
BUDS		
Picea excelsa	4.0	Danilov, 1938

Unfortunately, the relative digestibility of different food sources is not known for different mammals. The large gastric caecum of many rodents has been suggested as a site of enzyme systems capable of extracting energy from β-linked carbohydrates of fungal cell walls (C. Smith, 1965). Our impression from examining stomach and fecal contents of several hundred small mammal mycophagists is that fungal cell cytoplasm is readily digested, cell walls are sometimes digested, and spores are not digested at

TABLE 5. Chemical composition of dried plant parts and meat.

Plant Species	% Dry Weight Protein	Fat	Carbohydrate	Ash	Source
FUNGI					
Agaricus bisporus	48-62	1-2	—	7	Singer, 1961
Amillaria mellea	16	—	76	8	Singer, 1961
Boletus edulis	32-35	5	58-59	6-8	Singer, 1961
Clavaria flava	19	2	47	5	Winton and Winton, 1935
Hygrophorus, Amillaria, Russula, Clitocybe, Amanita, Tricholoma, Pholiota sp.	12-27	—	—	—	Miller and Halls, 1969
Hygrophorus, Amanita sp.	23	—	—	—	Miller and Halls, 1969
Lactarius deliciosus	27	7	28	6	Singer, 1961
Lentinus edodes	19	5	54	3	Singer, 1961
Marasmius oreades	35-43	2-4	34	10	Singer, 1961
Morchella esculenta	34-35	2	46-47	9-11	Singer, 1961
Morchella sp.	30	—	—	—	Mendel, 1898
Morchella, Rhizopogon, Cortinarius, Lactarius Amanita, Clitocybe sp.	30	—	—	—	Miller and Halls, 1969
Pleurotus cretacius	21	—	—	—	Winton and Winton, 1935
Saccharomyces cerevisiae	12	<1	21	—	Hodgman, *et al.*, 1963
Suillus granulatus	14	2	70	6	Singer, 1961
Suillus grevillei	21	2	64	6	Singer, 1961
Suillus luteus	20	4	53	6	Singer, 1961
Tricholoma favovirens	15-18	—	71-78	7-11	Singer, 1961
Tuber melanosporum	25-26	2	39-46	8	Andreotti and Casoli, 1968
NUTS					
Chestnut kernels	11	7	72	2	Hodgman, *et al.*, 1963 Chapman and Baumgartner, 1939
Butternut kernels	28	61	3	3	Winton and Winton, 1932
Black walnut kernels	28-30	56-58	6	2	Winton and Winton, 1932 Chapman and Baumgartner, 1939
Pecan kernels	10-11	70-75	10	2	Winton and Winton, 1932
Hickory kernels	13-20	65-70	6-9	2	Winton and Winton, 1932
Filbert kernels	16-17	63-65	10-13	2	Winton and Winton, 1932
Beechnut kernels	22	42-57	19	3-4	Winton and Winton, 1932 Chapman and Baumgartner, 1939
MEAT					
Chipped beef	30	6	<1	—	Hodgman, *et al.*, 1963

all. Spores presumably contain concentrated energy sources, as indicated by the relatively high caloric values of gills or tubes of mushrooms as compared to the somatic parts (Table 4) and by the high lipid content seen in spores of some fungi (Gerdemann and Trappe, 1974). However, reports of squirrels eating caps and gills of mushrooms while leaving the stems (Hatt, 1929; Ognev, 1940; C. Smith, 1965) probably reflect palatability rather than selection for food value.

Aside from their caloric value, some of the diverse organic compounds of fungi may be important in small mammal physiology. For example, ergosterol, a possibly important source of mammalian hormone precursors, occurs widely in the higher fungi

and ranges from about 0.2 to 0.5 percent of the dry weight of fleshy fungi (Milazzo, 1965; Shivrina *et al.,* 1968; Catalfomo and Trappe, 1970). Fungi commonly contain other steroids, triterpenes, amines, indoles, and phenols (Catalfomo and Trappe, 1970) of unknown but potential use to mammals. Vitamins such as biotin, niacin, pantothenic acid, and riboflavin are produced in significant amounts by some fleshy fungi (Shemakhanova, 1967). On a fresh weight basis, mushrooms have higher concentrations of niacin and riboflavin than most nuts, fruits, and leaf vegetables and equal or excel most meats in this regard (Proudfit and Robinson, 1950).

Fungal tissues effectively accumulate nonmetallic and metallic elements. Stark (1972) found that sporocarps of five fungal species contained substantially higher concentrations of Cu, N, P, and Zn than did pine needles (dry wt. basis). At least some of the five also contained higher concentrations of Ca, Fe, K, Mg, and Na. Fungal rhizomorphs were also high in concentrations of these elements, e.g., 180 times as much Fe as pine needles.

The overall quality of fungi as a food source for small mammals has not been experimentally assessed. Tevis (1952) reported that *Eutamias* stomachs containing only fungi were always heavier than those of animals feeding on non-fungal material. He also found that when chipmunks began to acquire hibernation fat, those eating fungi became fat sooner. But Naumov's report of squirrels starving to death while gorged with *Polyporus betulinus* Fr. suggests that some fungi may have very little food value (Ognev, 1940), at least for some mammals.

Cyclic over-population of mammals and poor seed crops probably periodically enhance the importance of mycophagy in reducing food stress (Lampio, 1967; Ognev, 1940; Rajala and Lampio, 1963). The effect of poor mast crops, traditionally considered a key factor in regulating squirrel populations, might be moderated in good mushroom years (Baumgartner, 1939; Brown and Yeager, 1945; Stienecker and Browning, 1970; Uhlig, 1955; and others). Seasonal buildup of rodent populations, together with the seasonality of fungal fruiting, might explain the increased seasonal use of *Endogone* by *Peromyscus maniculatus, Microtus longicaudus, Clethrionomys gapperi, Phenacomys intermedius,* and *Zapus princeps* (Williams and Finney, 1964).

Fungal Toxins and Mycophagy

Feeding trials and field observations of *Amanita muscaria, Amanita phalloides, Lactarius rufus,* and *Lactarius torminosus* consumption by squirrels indicate that they and presumably other rodents can safely eat mushrooms considered poisonous to man (Ballou, 1927; Cram, 1924; Hastings and Mottram, 1916; Hatt, 1929; Klugh, 1927; Metcalf, 1925). With this evidence in mind, Walton's (1898) observation, "For thirteen years I have made use of the varieties of mushrooms selected by squirrels and wood mice as edible. . .," should be taken skeptically. He was lucky to have escaped poisoning.

We have found no reports on poisoning of small mammals by fungi in the wild. One prime reason may be that no one has seriously studied the matter. Several hypotheses might be proposed, among them that (A) no fungi are poisonous to small mammals; (B) mammals can detect toxins by taste, smell, or in some other way; or (C) mammals are poisoned by some fungi, but when poisoning occurs, they seclude themselves before symptoms become evident to observers.

Hypothesis A was supported by Ford (1908, 1910), who suggested that herbivore alimentary canals can neutralize poisons which are highly toxic if administered by subcutaneous or interperitoneal inoculation. However, chickens and a cow are reported to have died after eating sporocarps of *Amanita* sp. (Ballou, 1927). Recently it has been demonstrated that a number of toxins each with different properties are responsible for mushroom poisoning symptoms (Litten, 1975). The *Amanita* toxin phalloiden, for instance, is not toxic when given orally, but mice given *Amanita* whole toxic extract containing myriaphalloisins die in a few hours to four days.

Hypothesis B seems a reasonable possibility, considering the selective pressure against genetic lines given to feasting on poisonous fungi. Hypothesis C also seems reasonable, especially since most mycotoxins require some incubation time before symptoms are expressed: mushroom poisoning of humans often does not arouse symptoms for several hours after ingestion. Hypothesis A has been proven wrong for a limited number of mammals; B and C remain to be tested.

Mycophagists as Disseminators of Fungi

Mycophagy serves in fungal dissemination by physical transport of spores and hypothetically, at least in some cases, by breaking spore dormancy. Most epigeous fungi, even the coprophilous species, are adapted for aerial or water transport of spores; mycophagy would seem incidental to primary dispersal mechanisms (Ingold, 1953). Of course, mushrooms hung in trees by squirrels are exposed to air currents that could carry spores farther than those at the ground surface. Mycorrhizal species or root pathogens may gain some strategic advantage over aerial dissemination if spores are eaten and then excreted near susceptible host roots by burrowing mycophagists.

Hypogeous fungi, on the other hand, are clearly dependent on mycophagy for physical transport. They fruit underground, their spore-bearing tissues are typically enclosed in a persistent peridium, and for the most part they do not forcibly discharge their spores. Even those which can forcibly discharge spores, such as the truffle relative, *Geopora cooperi* Harkn. (Burdsall, 1965), must be dug up and opened above ground by an animal to release spores to air currents (Korf, 1973).

The phycomycetous fungi of the family Endogonaceae deserve special mention because they have been found so often in small rodent stomachs. The various species may be epigeous or hypogeous and may form sporocarps or be borne as individual spores in soil. At present, only the sporocarp-forming species have been found in rodent stomachs. Whether epigeous or hypogeous, the sporocarps are typically compact clusters of very large spores devoid of discharge mechanisms. Presumably, these sporocarps are strongly dependent on mycophagy for transport. Spores borne singly in soil, on the other hand, may be eaten by insects or arthropods but also can be transported by any of the forces that move soil (Gerdemann and Trappe, 1974).

The effects of passage through a digestive tract on spore germination are unknown for most fungi. In general, spores of coprophilous and xylophilous fungi germinate poorly or not at all under any circumstances (Fries, 1943; Benedict *et al.,* 1967). The relatively few reported successes in inducing germination of spores of ectomycorrhizal fungi entailed treatments such as low temperature, alternate wetting and drying, soil extracts, co-culture with other organisms, slug digestive enzymes, or exposure to living roots (Sussman and Halversen, 1966; Bowen and Theodorous, 1974; Lamb and Richards,

1974). Of the Endogonaceae, chlamydosporic species which form vesicular-arbuscular mycorrhizae germinate readily without special treatment; one species has been shown to be viable after passage through a *Microtus* digestive tract (Trappe and Maser, 1976). No one has yet succeeded in germinating spores of those that occur only in sporocarps, at least some of which are ectomycorrhizal species (Gerdemann and Trappe, 1974).

Mycophagy would subject ingested fungal spores to body heat, enzymatic action, and co-culture with the myriad microorganisms of digestive tracts and feces. The process has not been demonstrated to affect spore dormancy as yet. Indeed root exudates appear to induce germination of some hypogeous mycorrhizal fungi without mycophagy (Palenzona, 1969; Bowen and Theodorous, 1974). Since essentially no research has been reported on the physiological effects of mycophagy on spores, the question remains moot.

Mycophagy in Ecosystem Analysis

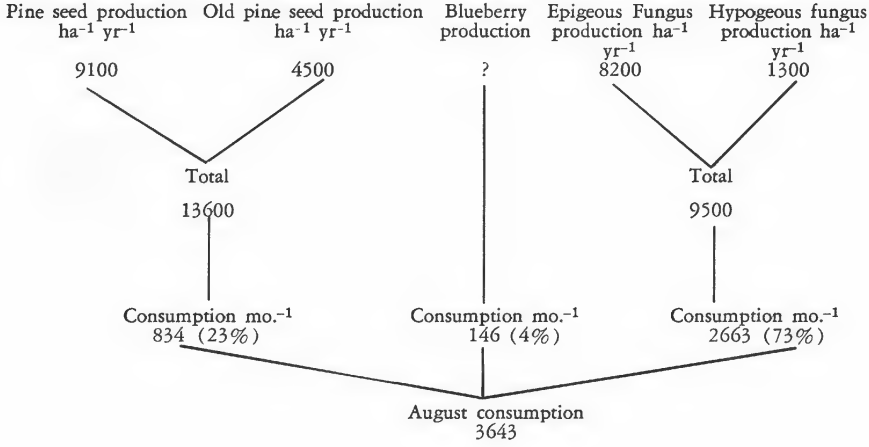
Invertebrates and vertebrates that feed wholly or in part on fungi have been arbitrarily categorized either as herbivores or fungal decomposers. No generalization fits comfortably, however, because the fungi may be saprophytes, biotrophic or necrotrophic symbionts, or predators (Harley, 1971; Lewis, 1973). Although necrotrophic symbionts may be considered "living tissue saprophytes" for purposes of ecosystem modeling, the biotrophic symbionts such as mycorrhizal fungi pose a special problem: the structural and physiological interdependence of fungus and host preclude their conceptual separation either physically or functionally.

One solution to this problem is to consider mycorrhizal fungi as extensions of the host root system, since the fungi are essential to nutrient absorption by the host and the fungi obtain their energy from the host much as if they were indeed root tissue. Thus the mycorrhizal fungi can be regarded as organs of producer plants. Mycophagists that feed on mycorrhizal fungi are then grazers. Grazing of mycorrhizal fungi accounts for about 75 percent of the small mammal mycophagy in terms of the reports listed later in this paper, evaluated as known or presumed mycorrhizal taxa (Trappe, 1962, 1971). If only reports of stomach contents are considered, the percentage is considerably higher. Mycophagy of saprophytes, necrotrophic symbionts, or predators, on the other hand, can be regarded as part of the decomposer process and accounts for about 25 percent of the reports. Many, perhaps most mycophagists feed on both categories of fungi and thereby participate in both processes.

Small mammal mycophagy seems surely to be a significant energy transfer process in ecosystems, but it remains to be quantitatively assessed. We are aware of only one paper with enough information to present a small mammal-fungus carbon budget for a short period: C. Smith (1965) estimated the caloric consumption of different food sources by the red squirrel *(Tamiasciurus hudsonicus)* for the month of August in western Washington. During this time, mycophagy accounted for about 73 percent of the squirrels' caloric intake, even though coniferous seeds and blueberries were also available (Fig. 1). Data from several other papers were not usable since percent volume and frequency values reported are useless without estimates of food consumption, weight, caloric value, stomach size, food density, etc. Modeling can not proceed until integrated studies on mycophagist food habits and fungal production are completed.

Despite inadequate information, mycophagy is clearly important to mammals and fungi alike. More extensive and definitive information is badly needed, particularly for understanding the dynamics of small mammal populations and for ecosystem modeling; nutrient flow is not a simple matter of diffusion through arbitrarily generalized functional groups such as primary producers, consumers, or decomposers.

Figure 1. *Tamiasciurus hudsonicus* caloric (kcal. 1000 gm^{-1}) consumption for August. (Smith, C., 1965) Percent of August consumption enclosed in parentheses.



The Reciprocal Lists

The literature reports of small mammal mycophagy are compiled in the following lists by taxa of both fungi and mammals. The lists are intended to provide a broad overview indexed to the original sources. Because any such listing is subject to limitations, restraint should be used in drawing detailed inferences from the lists themselves. Use them only as portals to the original literature. Keep in mind that the lists exclude lichens; that while coverage is almost complete for the North American literature, several references from other parts of the world could not be located; and that some taxa undoubtedly have been misidentified by some original authors.

No single system of taxonomy enjoys complete acceptance for either the fungi or the mammals. We have accordingly followed the classification and nomenclature of the more comprehensive compendia where possible, recognizing that many readers may prefer a somewhat different system. The fungal classification has been drawn from various sources, including Singer (1962) for Agaricales, Overholts (1953) for Polyporaceae, and Smith (1951) for Gasteromycetes. Mammal classification follows Hall and Kelson (1959), Jackson (1928), Johnson (1968), and Johnson and Ostenson (1959) for North American species and Ognev (1940, 1950) for Eurasian species.

The lists are alphabetical except for classes and orders. All known synonyms of a taxon have been cross-indexed to a single name; we do not intend any novel taxonomic decisions in this process, since the conclusions were drawn entirely from the literature, not from personal examination of types or other specimens.

Fungi listed with asterisk have been reported as demonstrated or probable mycorrhizal species in Trappe (1962, 1971), Gerdemann and Trappe (1974), or elsewhere.

Fungi and the Animals That Eat Them

CLASS PHYCOMYCETES
Unspecified taxa: *Potorous tridactylus apicalis* (Guiler, 1971).
ORDER OOMYCETALES
See Class Phycomycetes. Apparently this order has never been used.
ORDER MUCORALES
FAMILY ENDOGONACEAE
Endogone spp.: *Blarina brevicauda* (Hamilton, 1941b; Linzey and Linzey, 1973; Whitaker, 1962; Whitaker and Ferraro, 1963); *Clethrionomys gapperi gapperi* (Linzey and Linzey, 1973; Whitaker, 1962; Williams and Finney, 1964); Cricetidae (Dowding, 1959). *Eutamias* spp. Dowding, 1955, 1959; Whitaker, 1962); *Lagurus curtatus* (Whitaker, 1962); *Microtus chrotorrhinus* (Linzey and Linzey, 1973); *M. longicaudus* (Williams and Finney, 1964; *M. ochrogaster* (Zimmermann, 1965, 1966); *M. oeconomus macfarlandi* (Dowding, 1955; Whitaker, 1962); *M. pennsylvanicus* (Whitaker, 1962; Zimmermann, 1966); *M. pinetorum* (Linzey and Linzey, 1973; Whitaker, 1962); *Mus musculus* (Calhoun, 1941; Whitaker, 1962, 1966); *Napaeozapus insignis insignis* (Linzey and Linzey, 1973; Whitaker, 1962, 1963a); *Ochotona* spp. (Dowding, 1959); *O. princeps* (Whitaker, 1962; Zimmermann, 1965); *Onychomys leucogaster* (Whitaker, 1962); *Oryzomys palustris* (Negus, Gould, and Chipman, 1961); *Peromyscus gossypinus* (Calhoun, 1941; Whitaker, 1962); *P. lecucopus* (Calhoun, 1941; Linzey and Linzey, 1973; Whitaker, 1962, 1963b, 1966); *P. leucopus noveboracensis* (Hamilton, 1941b); *P. maniculatus* (Dowding, 1955; Linzey and Linzey, 1973; Whitaker, 1962; Williams and Finney, 1964); *P. maniculatus bairdii* (Whitaker, 1966); *P. maniculatus gracilis* (Hamilton, 1941b); *Phenacomys intermedius* (Williams and Finney, 1964), Rodentia (Ingold, 1961, 1966; Kessler and Blank, 1972); *Sorex* spp. (Thaxter, 1922); *S. bendirii* (Whitaker and Maser, 1976); *S. cinereus* (Whitaker, 1962); *S. fumeus* (Linzey and Linzey, 1973; Whitaker, 1962); *S. trowbridgii* (Whitaker and Maser, 1976); *S. vagrans* (Whitaker and Maser, 1976); *S. vagrans pacificus* (Whitaker and Maser, 1976); *S. vagrans yaquinae* (Whitaker and Maser, 1976); *Soricidae* (Dowding, 1959); *Synaptomys cooperi cooperi* (Conner, 1960; Hamilton, 1941a, 1942; Hatt, 1930; Linzey and Linzey, 1973; Whitaker, 1962); *S. cooperi gossii* (Burt, 1928; Hamilton, 1941b); Talpidae (Dowding, 1959); *Zapus hudsonicus* (Whitaker, 1962); *Z. princeps* (Williams and Finney, 1964); *Z. trinotatus* (Whitaker, 1962).
**E. flammicorona* Trappe and Gerdemann: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**E. lactiflua* Berk. and Broome: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974); *Zapus trinotatus* (Gerdemann and Trappe, 1974).
E. pisiformis Link *ex* Fries: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
E. macrospora: See *G. macrocarpa. (E. macrospora* was an erroneous citation for *E. macrocarpa).*
**Glomus caledonius* (Nicol. and Gerd.) Trappe and Gerdemann: *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**G. fasciculatus* (Thaxt. *sensu* Gerdemann) Gerdemann and Trappe: *Clerthrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Lagurus curtatus* (Dowing, 1955); *Microtus pennsylvanicus* (Bakerspigel, 1956, 1958; Whitaker, 1962); *Ochotona princeps* (Dowding, 1955); *Onychomys leucogaster* (Dowding, 1955); *Peromyscus maniculatus* (Bakerspigel, 1956, 1958; Dowding, 1955; Whitaker, 1962); *Sciurus aberti* (Stephenson, 1975); *Zapus princeps* (Bakerspigel, 1956; Whitaker, 1962); *Z. trinotatus* (Gerdemann and Trappe, 1974).
**G. macrocarpus* Tul. and Tul.: *Blarina* spp. (Hamilton, 1941b); *B. brevicauda* (Diehl, 1939); *Clethrionomys* spp. (Hamilton, 1941b); *C. gapperi gapperi* (Diehl, 1939); *Peromyscus* spp. (Hamilton, 1941b); *P. leucopus novoboracensis* (Diehl, 1939); *P. maniculatus* (Harling and McClaren, 1970); *Sorex cinereus* (Diehl, 1939; Hamilton, 1941b); *S. fumeus* (Diehl, 1939; Hamilton, 1941b); *Synaptomys cooperi cooperi* (Diehl, 1939); *S. cooperi gossii* (Hamilton, 1941b).
**G. macrocarpus* Tul. and Tul. *var. *macrocarpus: Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**G. microcarpus* Tul. and Tul.: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974).
**G. monosporus* Gerdemann and Trappe: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Zapus trinotatus* (Gerdemann and Trappe, 1974).
G. pulvinatus (Henn.) Trappe and Gerdemann: *Zapus princeps* (Dowding, 1955; Whitaker, 1962).
**Sclerocystis rubiformis* Gerdemann and Trappe: *Clethrionomys californicus californicus* (Gerdemann and Trappe, 1974); *Peromyscus maniculatus* (Gerdemann and Trappe, 1974); *Zapus trinotatus* (Gerdemann and Trappe, 1974).

CLASS ASCOMYCETES
ORDER PLECTASCALES
FAMILY ELAPHOMYCETACEAE
Elaphomyces spp.: *Neotoma fuscipes annectens* (Parks, 1922); Rodentia (Ingold, 1961, 1966; Reess and Fisch, 1887); *Sciurus aberti* (Stephenson, 1975).
**E. granulatus* Fr.: Leporidae (Hawker, 1954); Rodentia (Hastings and Mottram, 1916; Hawker, 1954; Ingold, 1953); Sciuridae (Bulle-, 1922; Dowding, 1959); *Sciurus carolinensis carolinensis* (Ingold, 1973); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
ORDER DOTHIDEALES
FAMILY DOTHIDEACEAE
Dibotryon spp: *Sciurus carolinensis carolinensis* (Dudderar, 1967).
ORDER HYPOCREALES
FAMILY HYPOCREACEAE
Hypomyces spp.: *Tamiasciurus hudsonicus hudsonicus* (Seton, 1928).
ORDER PEZIZALES
FAMILY HELVELLACEAE
Helvella spp.: *Oryctolagus cuniculus* (Kumerloeve, 1956).
H. lacunosa Afz. *ex* Fr.: *Neotoma fuscipes* (Linsdale and Tevis, 1951).
H. mitra: See *H. lacunosa.*
Paxina acetabulum (L. *ex* St. Amans) Kuntze: *Neotoma fuscipes* (Linsdale and Tevis, 1951).
FAMILY MORCHELLACEAE
Tamiasciurus hudsonicus hudsonicus (Buller, 1922).
Morchella spp.: *Lepus europaeus* (Kumerloeve, 1956).
FAMILY PEZIZACEAE
**Geopora cooperi* Harkness: *Sciurus aberti aberti* (Stephenson, 1975).
Peziza spp.: *Neotoma fuscipes* (Linsdale and Tevis, 1951); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
P. emileia Cke: Neotoma fuscipes (Linsdale and Tevis, 1951).
ORDER TUBERALES
Peromyscus boylei (Jameson, 1952); *Spermophilus* spp. (Bessey, 1935); *Tamiasciurus douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
FAMILY TUBERACEAE
Leporidae (Kavaler, 1965); *Neotoma* spp. (Smith, 1938); Rodentia (Christenson, 1951; Kavaler, 1965; Lilly and Barnett, 1951; Mehrotra, 1967; Smith, 1938); Sciuridae (Kavaler, 1965).
Balsamia spp.: *Clethrionomys glareolus* (Drożdż, 1966).
**B. vulgaris* Vitt.: *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *S. vulgaris* (DuReau, 1912; Hatt, 1929).
**Fischerula subcaulis* Trappe: *Microtus oregoni* (Trappe, 1975).
Genea spp.: *Clethrionomys glareolus* (Drożdż, 1966).
Hydnotrya spp.: *Clethrionomys glareolus* (Drożdż, 1966).
Tuber spp.: *Clethrionomys glareolus* (Drożdż, 1966); Geomyidae (Parks, 1922); *Neotoma fuscipes* (Linsdale and Tevis, 1951); Rodentia (Ingold, 1961, 1966); *Sciurus aberti aberti* (Keith, 1965; Stephenson, 1975).
**T. aestivum* Vitt.: Rodentia (Hawker, 1954).
T. candidum Harkn: see *T. rufum* var. *nitidum.*
**Tuber rufum* var. **nitdium* (Vitt.) Fischer: *Neotoma* spp. (Parks, 1921); Rodentia (Parks, 1921).
CLASS BASIDIOMYCETES
ORDER UREDINALES
Peromyscus leucopus (Calhoun, 1941).
FAMILY PUCCINIACEAE
Peridermium harknessii Moore: *Tamiasciurus hudsonicus hudsonicus* (Smith, C. 1965).
FAMILY MELAMPSORACEAE
Cronartium ribicola A. Fisch.: *Sciuridae* (Spaulding, 1922); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
ORDER TREMALES
FAMILY DACRYMYCETACEAE
Calocera viscosa (Fr.) Fr.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932).
ORDER AGARICALES
Sciurus vulgaris leucourus (Barrett-Hamilton and Hinton, 1921).
FAMILY AGARICACEAE
Neotoma cinerea orolestes (Finley, 1958); *N. floridana magister* (Newcombe, 1930); *N. fuscipes annectens* (Parks, 1922); *Sciurus carolinensis carolinensis* (Styan, 1946); *S. niger niger* (Baumgartner, 1939a, 1939b).
Agaricus spp.: *Neotoma floridana magister* (Newcombe, 1930); *Sciurus aberti aberti* (Keith, 1965).
A. campestris L. *ex* Fr.: *Potorous tridactylus apicalis* (Guiler, 1971); *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
Coprinus spp.: *Blarina brevicauda* (Hamilton, 1930); *Didelphis virginiana* (Hamilton, 1958).
Lepiota spp.: *Sciurus aberti aberti* (Keith, 1965).
L. naucinoides: See *Leucoagaricus naucinus.*

Leucoagaricus naucinus (Fr.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).
Mycena epipterygia (Scott. *ex* Fr.) S. F. Gray: *Leporidae* (Hastings and Mottram, 1916).
Psalliota campestris: See *Agaricus campestris.*
FAMILY AMANITACEAE
Amanita spp.: Mammalia (Miller and Halls, 1969); Sciuridae (Miller and Halls, 1969); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hamilton, 1939, Smith, 1968); *T. hudsonicus minnesota* (Hamilton, 1943).
**A. muscaria* (L. *ex* Fr.) Pers. *ex* Hooker: Rodentia (Hastings and Mottram, 1916); Sciuridae (Hastings and Mottram, 1916); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927; Krieger, 1967; Metcalf, 1925; Rue, 1967).
**A. phalloides* (Vaill. *ex* Fr.) Secr.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
**A. rubescens* (Pers. *ex* Fr.) S. F. Gray: Leporidae (Hastings and Mottram, 1916).
**A. vaginata* (Bull. *ex* Fr.) Vitt.: *Sciurus aberti aberti* (Keith, 1965); *Tamias striatus lysteri* (Allen, 1938, Fraleigh, 1929); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Aminitopsis vaginata varialba: See *Amanita vaginata.*
Pluteus atricapillus (Secr.) Sing.: *Neotoma fuscipes* (Linsdale and Tevis, 1951); *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
P. cervinus: See *P. atricapillus.*
P. nanus (Pers. *ex* Fr.) Kumm.: *Sciurus vulgaris exalbidus* (Ognev, 1940).
FAMILY BOLETACEAE
Neotoma fuscipes annectens (Parks, 1922); Rodentia (Miller and Halls, 1969); Sciuridae (Miller and Halls, 1969).
Boletinus cavipes: See *Suillus cavipes.*
**B. pictus* (Peck) Peck: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Boletus spp.: *Eutamias quadrimaculatus* (Tevis, 1952); *Lemmus lemmus* (Ognev, 1948); *Neotoma floridana magister* (Newcombe, 1930; Poole, 1940); Sciuridae (Odell, 1926); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Cross, 1942; Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922; Klugh, 1927; Krieger, 1967; Seton, 1929; Smith, 1968).
B. badius: See *Xerocomus badius.*
B. bovinus: See *Suillus bovinus.*
**B. calopus* Fr.: Sciuridae (Cooke, 1890); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).
B. castaneus: See *Gyroporus castaneus.*
B. chrysenteron: See *Xerocomus chrysenteron.*
**B. edulis* Bull. *ex* Fr.: Rodentia (Hastings and Mottram, 1916); *Sciurus vulgaris* (Ognev, 1940).
B. flavidus: See *Suillus flavidus.*
**B. impolitus* Fr.: Sciuridae (Cooke, 1890); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).
B. luteus: See *Suillus luteus.*
**B. mirabilis* Murr.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
B. pachypus: See *B. calopus.*
B. pallidus Frost: *Neotoma floridana magister* (Poole, 1940).
B. piperatus: See *Suillus piperatus.*
B. rufus: See *Leccinum aurantiacum.*
B. scaber: See *Leccinum scabrum.*
B. subtomentosus: See *Xerocomus subtomentosus.*
B. variegatus: See *Suillus variegatus.*
B. versipellis Fr.: See *Leccinum versipellis.*
**Gyroporus castaneus* (Bull. *ex* Fr.) Quél.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
**Leccinum aurantiacum* (Bull.) S. F. Gray: *Sciurus vulgaris* (Ognev, 1940); *S. vulgaris exalbidus* (Ognev, 1940; Stakhrovskii, 1932).
**L. scabrum* (Fr.) S. F. Gray: Sciuridae (Massee, 1913); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *S. vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *S. vulgaris exalbidus* (Ognev, 1940); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hatt, 1929).
**L. versipellis* (Fr.) Snell: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
**Suillus bovinus* (L. *ex* Fr.) Kuntze: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *S. vulgaris exalbidus* (Ognev, 1940); *Tamiasciurus husonicus hudsonicus* (Hatt, 1929).
**S. cavipes* (Opat.) A. H. Sm. and Thiers: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
**S. flavidus* (Fr.) Sing.: Rodentia (Hastings and Mottram, 1916).
**S. granulatus* (Fr.) Kuntze: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
**S. lakei* (Murr.) A. H. Sm. and Thiers: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
**S. luteus* (L. *ex* Fr.) S. F. Gray: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *S. vulgaris exalbidus* (Ognev 1940); *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

S. piperatus (Bull. *ex* Fr.) Kuntze: *Sciurus vulgaris exalbidus* (Ognev, 1940).
S. subolivaceus A. H. Sm. and Thiers: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
S. tomentosus (Kauffm.) Sing., Snell, and Dick: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
S. variegatus (Sw. *ex* Fr.) Kuntze: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensus* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Xerocomus badius (Fr.) Kühner *ex* Gilbert: Leporidae (Buller, 1922); Rodentia (Hastings and Mottram, 1916).
X. chrysenteron (Bull. *ex* St. Amans) Quél.: Rodentia (Hastings and Mottram, 1916); *Sciurus vulgaris exalbidus* (Ognev, 1940).
X. subtomentosus (L. *ex* Fr.) Quél.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *S. vulgaris exalbidus* (Ognev, 1940).

FAMILY COPRINACEAE

Hypholoma spp.: See *Psathyrella* spp.
H. fasiculare: See *Naematoloma fasiculare* in Strophariaceae.
Psathyrella spp.: *Sciurus aberti aberti* (Keith, 1965); *Tamiasciurus hudsonicus hudsonicus* (Seton, 1929).

FAMILY CORTINARIACEAE

Cortinarius spp.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hardy, 1949; Hatt, 1929; Seton, 1929; Smith, C., 1965).
C. collinitus (Pers. *ex* Fr.) Fr.: Rodentia (Hastings and Mottram, 1916).
C. distans Peck: Rodentia (Miller and Halls, 1969).
C. varius (Schaeff. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
Flammula sapinea: See *Gymnopilus sapineus.*
Gymnopilus sapineus (Fr.) Maire: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Inocybe spp.: *Neotoma floridana magister* (Newcombe, 1930; Poole, 1940); *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Rozites caperata (Pers. *ex* Fr.) Karst.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

FAMILY CREPIDOTACEAE

Crepidotus malachius: See *C. nephrodes.*
C. nephrodes (Berk. and Curt.) Sacc.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).

FAMILY GOMPHIDACEAE

Chroogomphus rutilus: See *Gomphidius rutilus.*
C. tomentosus: See *Gomphidius tomentosus.*
Gomphidius glutinosus (Shaeff. *ex* Fr.) Fr.: *Sciurus vulgaris exalbidus* (Ognev, 1940).
G. rutilus (Schaeff. *ex* Fr.) Lund. and Nannf.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
G. subroseus Kauffm.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
G. tomentosus Murr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

FAMILY HYGROPHORACEAE

Hygrocybe miniata (Scop. *ex* Fr.) Kumm.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
Hygrophorus chrysodon (Batsch *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
H. hypothejus (Fr.) Fr.: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
H. miniatus: See *Hygrocybe miniata.*
H. pudorinus (Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Odell, 1925).

FAMILY PAXILLACEAE

Hygrophoropsis aurantiaca (Wulf *ex* Fr.) Maire: Leporidae (Hastings and Mottram, 1916); Rodentia (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Paxillus atrotomentosus (Batsch *ex* Fr.) Fr.: Rodentia (Hastings and Mottram, 1916).
P. involutus (Batsch *ex* Fr.) Fr.: Leporidae (Hastings and Mottram, 1916); Rodentia (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

FAMILY RUSSULACEAE

Clethrionomys rutilus mikado (Murata, 1976).
Lactarius spp.; Rodentia (Miller and Halls, 1969); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
L. deliciosus (L. *ex* Fr.) S. F. Gray: *Sciurus carolinensis carolinensis* (Barkalow and Shorten, 1973); *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
L. lignyotus (Fr. *ex* Fr.) Fr.: *Clethrionomys gapperi gapperi* (Hamilton, 1941b).
L. necator (Bull. *em.* Pers. *ex* Fr.) Karst.: Rodentia (Hastings and Mottram, 1916).
L. piperatus (L. *ex* Fr.) S. F. Gray: Rodentia (Miller and Halls, 1969); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hardy, 1949; Hatt, 1929).
L. rufus (Scop. *ex* Fr.) Fr.: Rodentia (Hastings and Mottram, 1916).
L. torminosus (Schaeff. *ex* Fr. S. F. Gray: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932).
L. turpis: See *Lactarius necator.*
L. uvidus (Fr. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
Russula spp.: *Clethrionomys glareolus* (Drożdż 1966); *Lemmus lemmus* (Ognev, 1948); *Napa-*

eozapus insignis insignis (Sheldon, 1934); *Neotoma floridana magister* (Newcombe, 1930; Poole, 1940); Sciuridae (Dowding, 1955); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Cross, 1942; Dudderar, 1967; Murrill, 1910); *Tamias striatus lysteri* (Allen, 1938; Fraleigh, 1929; Sheldon, 1936); *Tamiasciurus hudsonicus fremonti* (Hatt, 1943); *T. hudsonicus hudsonicus* (Buller, 1920, 1922; Klugh, 1927).

**R. adusta* (Pers. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

**R. alutacea* (Pers. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

**R. bicolor* Burl.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. bicolor var. *constans:* See *Russula bicolor.*

R. bicolor var. *reticulispora:* See *Russula bicolor.*

**R. blackfordae* Peck: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. brevipes* Peck: *Tamiasciurus douglasi douglasi* (Smith, C., 1965).

**R. consobrina* (Fr. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. decorans* Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. delica: see *R. brevipes.*

R. depallens: See *Russula pulchella.*

R. disparilis Burl.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. emetica* (Schaeff. *ex* Fr.) Pers. *ex* Fr.: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* Hatt, 1929).

**R. emetica* ssp. **fragilis* (Pers. *ex* Fr.) Sing.: *Tamiasciurus hudsonicus* (Smith, C., 1965).

R. fragilis: See *Russula emetica* ssp. *fragilis.*

R. mariae Peck: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

*R. *nigricans* (Bull. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. ochroleuca* (Pers. *ex* Fr.: *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).

R. pallidostraminea nom. prov.: Tamiasciurus hudsonicus hudsonicus (Smith, C., 1965).

**R. pulchella* Borsc.: *Tamiaciurus hudsonicus hudsonicus* (Smith, C., 1965).

**R. rosea* Quél.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. rosipes (Secr.) Bres.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

**R. rubra* (Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

**R. xerampelina* (Schaeff. *ex* Secr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

R. xerampelina var. isabelliniceps: See *R. xerampelina.*

FAMILY STROPHARIACEAE

Kuehneromyces mutabilis (Schaeff. *ex* Fr.) Sing. and A. H. Sm.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932).

Naematoloma fasiculare (Huds *ex* Fr.) Karst.: *Sciurus vulgaris* (Moffat, 1923); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hatt, 1929).

Pholiota spp.: *Sciurus vulgaris* (Ognev, 1940).

P. carbonaria (Fr.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

P. discolor (Pk.) Sacc.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968).

P. lenta (Pers. *ex* Fr.) Sing.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965).

P. mutabilis: See *Kuehneromyces mutabilis.*

FAMILY TRICHOLOMATACEAE

Armillaria spp.: *Sciurus vulgaris* (Ognev, 1940).

A. mellea (Vahl in Fl. Dan. *ex* Fr.) Karst.: Sciuridae (Miller and Halls, 1969); *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1920, 1922; Hatt, 1929).

Clitocybe spp.: *Eutamias quadrimaculatus* (Tevis, 1952); *Sciurus vulgaris* (Ognev, 1940); *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

C. brumalis (Fr.) Quél.: Leporidae (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

C. maxima (Fl. Wett. *ex* Fr.) Kumm.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

C. monodelpha Morg.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

**C. odora* (Bull. *ex* Fr.) Kumm.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

C. virens: See *C. odora.*

Collybia dryophila (Bull. *ex* Fr.) Kumm.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).

C. maculata (A. and S. *ex* Fr.) Quél.: Rodentia (Hastings and Mottram, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).

C. radicata: See *Oudemansiella radicata.*

C. velutipes: See *Flammulina velutipes.*

Flammulina velutipes (Curt. *ex* Fr.) Sing.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain 1968).

Lentinus lepideus (Fr. *ex* Fr.) Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

**Lepista personata* (Fr. *ex* Fr.) Cke.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

Lyophyllum ulmarium (Bull. *ex* Fr.) Kühner: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).

Marasmius spp.: *Orcytolagus cuniculus* (Kumerloeve, 1956).

Oudemansiella radicata (Relh. *ex* Fr.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).

Tricholoma spp.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).

T. equestre: See *T. flavovirens.*

T. flavovirens (Pers. *ex* Fr.) Lund.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Odel, 1925).
T. personatum: See *Lepista personata.*
T. terreum (Schaeff. *ex* Fr.) Kumm.: *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916).
ORDER APHYLLOPHORALES
FAMILY CANTHARELLACEAE
Cantharellus aurantiacus: See *Hygrophoropsis aurantiaca* in Paxillaceae.
C. cibarius Fr.: *Sciurus vulgaris* (Ognev, 1940; Stakhrovskii, 1932); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922; Hatt, 1929; Klugh, 1927).
C. floccosus: See *Gomphus floccosus.*
Gomphus floccosus (Schw.) Sing.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
FAMILY CLAVARIACEAE
Clavaria spp.: *Neotoma floridana magister* (Newcombe, 1930; Poole, 1930); *Tamiasciurus hudsonicus hudsonicus* (Smith, 1968).
C. aurea: See *Ramaria aurea.*
C. flava: See *Ramaria flava.*
C. pyxidata: See *Clavicorona pyxidata.*
Clavicorona pyxidata (Fr.) Poty: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
Ramaria aurea (Fr.) Quél.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).
R. flava (Fr.) Quél.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Sparassis crispa Fr.: Leporidae (Hastings and Mottram, 1916).
FAMILY HYDNACEAE
Hericium caput-ursi (Fr.) Banker: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
Hydnum spp.: *Tamiasciurus hudsonicus hudsonicus* (Smith, 1968).
H. caput-ursi: See *Hericium caput-ursi.*
H. erinaceus Bull.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
H. fuligineo-violaceum Kalchb. in Fr.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
H. imbricatum L. *ex* Fr. *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
H. repandum L. *ex* Fr.: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
FAMILY POLYPORACEAE
Sciurus griseus griseus (Grinnel and Storer, 1924).
Daedalea spp.: *Sciurus carolinensis carolinensis* (Dudderar, 1967).
Fomes fomentarius (L. *ex* Fr.) Kickx: *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
F. pinicola (Swartz *ex* Fr.) Cooke: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Pleurotus spp.: *Sciurus niger niger* (Packard, 1956).
P. ostreatus (Jacq. *ex* Fr.) Kumm.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929; Klugh, 1927).
P. ulmarius: See *Lyophyllum ulmarium.*
Polyporus spp.: *Neotoma cinerea orolestes* (Warren, 1920); *Sciurus carolinensis carolinensis* (Dudderar, 1967; *Spermophilus lateralis* (Gordon, 1943); *Sylvilagus palustris paludicola* (Blair, 1936); *Tamiasciurus hudsonicus fremonti* (Hatt, 1943); *T. hudsonicus hudsonicus* (Hardy, 1949; Smith, 1968); *T. hudsonicus loquax* (Layne, 1954).
P. amarus Hedgc.: Sciuridae (Boyce, 1920); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
P. betulinus Bull. *ex* Fr.: Leporidae (Hastings and Mottram, 1916); *Sciurus vulgaris* (Ognev 1940); *Tamiasciurus hudsonicus hudsonicus* (Buller, 1922).
P. picipes Fr.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
P. sulphureus Bull. *ex* Fr.: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
P. varius Fr.: *Neotoma fuscipes* (Linsdale and Tevis, 1951).
Polysticus spp.: See *Polyporus* spp.
FAMILY STEREACEAE
Stereum hirsutum Willdenon *ex* Fr.: *Sciurus carolinensis carolinensis* (Murrill, 1910).
ORDER HYMENOGASTRALES
FAMILY HYMENOGASTRACEAE
Rodentia (Gäumann and Dodge, 1928).
Alpova diplophloeus (Zeller and Dodge) Trappe: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
Gautieria spp.: *Neotoma* spp. (Parks, 1919); *N. fuscipes annectens* (Parks, 1922); *Sciurus aberti aberti* (Stephenson, 1975); *S. griseus griseus* (Stienecker and Browning, 1970).
G. graveolens Vitt.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, 1965; Smith, C., 1965).
G. morchelliformis Vitt.: *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
Hydnangium spp.: *Neotoma fuscipes annectens* (Parks, 1922).
Hymenogaster spp.: *Blarina brevicauda* (Whitaker, 1962; Whitaker and Ferraro, 1963); *Clethrionomys gapperi gapperi* (Whitaker, 1962); *C. glareolus* (Drożdż, 1966); *Microtus oeconomus macfarlandi* (Whitaker, 1962); *Napaeozapus insignis insignis* (Whitaker, 1962, 1963a);

Neotoma fuscipes annectens (Parks, 1922); Rodentia (Ingold, 1961, 1966); *Zapus hudsonius* (Whitaker, 1962).
**H. tener* Berk.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Martellia spp.: *Sciurus aberti aberti* (Stephenson, 1975).
Rhizopogon spp.: *Clethrionomys glareolus* (Drożdż, 1966); Rodentia (Ingold, 1966; Miller and Halls, 1969); Sciuridae (Miller and Halls, 1969); *Sciurus aberti aberti* (Stephenson, 1975); S. *griseus griseus* (Stienecker and Browning, 1970).
R. diplophloeus: See *Alpova diplophloeus.*
**R. luteolus* Fr. and Nordh.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
**R. maculatus* Zeller and Dodge: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
**R. occidentalis* Zeller and Dodge: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
R. pachyphloeus: See *Alpova diplophloeus.*
R. provincialis: See *R. vulgaris.*
**R. roseolus* Corda *sensu* A. H. Sm.: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
**R. rubescens* (Tul.) Tul.: *Tamiasciurus douglasi douglasi* (Smith, C., 1965); *T. hudsonicus hudsonicus* (Smith, C., 1965).
**R. vinicolor* Sm.: *Tamiasciurus douglasi douglasi* (Fogel, 1976).
**R. viridis* Zeller and Dodge: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
**R. vulgaris* (Vitt.) M. Lange: *Tamiasciurus hudsonicus hudsonicus* (Smith, C., 1965).
**Truncocolumella citrina* Zeller: *Tamiasciurus douglasi douglasi* (Fogel, 1976); *T. hudsonicus hudsonicus* (Smith, C., 1965).
ORDER HYSTERANGIALES
FAMILY HYSTERANGIACEAE
Rodentia (Gaümann and Dodge, 1928).
Hysterangium spp.: *Neotoma* spp.: (Parks, 1919); *N. fuscipes annectens* (Parks, 1922); *Sciurus aberti aberti:* (Stephenson, 1975); *S. griseus griseus* (Stienecker and Browning, 1970).
FAMILY MELANOGASTRACEAE
Melanogaster spp.: *Clethrionomys glareolus* (Drożdż, 1966); *Neotoma* spp. (Parks, 1919); *N. fuscipes* (Linsdale and Tevis, 1951); *N. fuscipes annectens* (Parks, 1922); *Sciurus griseus griseus* (Stienecker and Browning, 1970).
**M. ambiguus* (Vitt.) Tul.: Sciuridae (Langham, 1916); *Sciurus carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus hudsonicus* (Hatt, 1929).
M. broomeianus Berk. *in* Tul.: Leporidae (Hawker, 1954).
M. variegatus (Vitt.) Tul. *emend.* Zeller and Dodge: *Microtus pennsylvanicus* (Bakerspigel, 1958); *Peromyscus maniculatus* (Bakerspigel, 1958).
M. variegatus var. *broomeianus:* See *M. broomeianus.*
ORDER LYCOPERDALES
Dasypus novemcinctus mexicanus (Kalmbach, 1944); Phascolomidae (Troughton, 1947).
FAMILY GEASTERACEAE
Geastrum spp.: *Tamias striatus griseus* (Schmidt, 1931).
FAMILY LYCOPERDACEAE
Neotoma albigula warreni (Finley, 1958); *Tamias striatus fisheri* (Tunis, 1971).
Castoreum spp.: Leporidae (Cleland, 1935); Marsupialia (Cleland, 1935).
C. radicatum Cke. and Mass.: Marsupialia (Cunningham, 1942).
Lycoperdon spp.: *Apodemus sylvaticus* (Miller, 1954); *Neotoma cinerea* (Dalquest, 1948); *N. cinerea occidentalis* (Taylor, 1920); *N. floridana magister* (Poole, 1940); *Oryctolagus cuniculus* (Kumerloeve, 1956); *Sciurus aberti aberti* (Keith, 1965); *S. carolinensis carolinensis* (Hastings and Mottram, 1916); *Tamiasciurus hudsonicus loquax* (Connor, 1960).
**L. gemmatum* Batsch: *Sciurus carolinensis carolinensis* (Nixon, Worley, and McClain, 1968); *S. niger niger* (Nixon, Worley, and McClain, 1968).
L. pyriforme Pers.: *Tamiasciurus hudsonicus hudsonicus* (Hardy, 1949).
Mesophellia spp.: Leporidae (Cleland, 1936; Cunningham, 1942); Marsupialia (Cleland, 1935; Cunningham, 1942).
M. arenaria Berk.: Leporidae (Cunningham, 1942); Macropodidae (Cunningham, 1942); Marsupialia (Cunningham, 1942); Permelidae (Cunningham, 1942).
M. pachythrix (Cke. and Mass.) Lloyd: Leporidae (Cleland, 1935).
ORDER SCLERODERMATALES
FAMILY SCLERODERMATACEAE
Scleroderma spp.: *Oryctolgus cuniculus* (Kumerloeve, 1956).
**S. citrinum* Pers.: *Neotoma floridana magister* (Newcombe, 1930).
S. hypogaeum Zeller: *Neotoma fuscipes* (Linsdale and Tevis, 1951).
S. vulgara: See *S. citrinum.*
MISCELLANEOUS REPORTS
Unnamed fungi: *Apodemus flavicollis* (Drożdż, 1966; Zemanek, 1972); *A. sylvaticus* (Hansson, 1970; 1971; Holišová, 1960; Southern, 1964); *Clethrionomys* spp. (Palmer, 1954; Walker, 1964); *C. gapperi athabascae* (Harper, 1956); *C. gapperi gapperi* (Connor, 1960; Doutt, Heppenstall, and Guilday, 1967; Jackson, 1961; Larrison, 1970; Linzey and Linzey, 1973); *C. gapperi paludicola* (Doutt, Heppenstall, and Guilday, 1967); *C. gapperi rhoadsii* (Connor, 1953); *C. gapperi rupicola* (Doutt, Heppenstall, and Guilday, 1967); *C. glareolus* (Hansson, 1969, 1971; Holišová, 1971, 1972; Miller, 1954; Ognev, 1950; Southern, 1964; Zem-

anek, 1972); *C. rufocanus* (Hansson, 1969); *Dasypus novemcinctus mexicanus* (Fitch, Goodrum, and Newman, 1952; Kalmbach, 1944; Miller and Halls, 1969); *Dicrostonyx groenlandicus* (Dunaeva and Kucheruk, 1941; Watson, 1956); *D. torquatus* (Ognev, 1948); *Didelphis virginiana* (Palmer, 1964; Sumner and Dixon, 1953); *Dipodomys* spp. (Cahalane, 1947; Palmer, 1954); *Eutamias* spp. (Cahalane, 1947; Gordon, 1943; Hamilton, 1939; Olin, 1961; Orr, 1949; Palmer, 1954; Walker, 1964); *E. cinereicollis cinereicollis* (Bailey, 1931); *E. minimus neglectus* (Hamilton, 1943); *E. minimus pictus* (Bailey, 1936); *E. quadrivittatus quadrivittatus* (Baliey, 1931; MacClintock, 1970); *E. speciosus* (Ingles, 1947; Tevis, 1953); *E. townsendii* (Larrison, 1970); *E. townsendii senex* (Bailey, 1936); *Glaucomys* spp. (Palmer, 1954); *G. sabrinus* (Cahalane, 1947; MacClintock, 1970; McKeever, 1960); *G. sabrinus fuscus* (Hamilton, 1943); *G. sabrinus macrotis* (Connor, 1960; Jackson, 1961); *G. volans* (Cahalane, 1947; Corbet, 1966; MacClintock, 1970; Ognev, 1940; Schwartz and Schwartz, 1959); *G. volans volans* (Connor, 1960); *Isoden obesulus* (Brazenor, 1950); *Lemmus lemmus* (Corbet, 1966; Marsden, 1964; Ognev, 1948); Leporidae (Rolfe and Rolfe, 1925); *Lepus europaeus* (Hansson, 1970); Macropodidae (Cleland, 1934); *Mastocomys* spp. (Walker, 1964); *Microdipodops* spp. (Cahalane, 1947); *Microtus agrestis* (Hansson, 1970, 1971); *M. pennsylvanicus* (Golley, 1960); *Neotoma* spp. (Hamilton, 1939); *N. cinerea* (Dalquest, 1948); *N. cinerea occidentalis* (Taylor, 1920); *N. cinerea orolestes* (Warren, 1942); *N. floridana* (Hall, 1955; Schwartz and Schwartz, 1959); *N. floridana attwateri* (Bailey, 1905; Rainey, 1956); *N. floridana magister* (Hamilton, 1943; Newcombe, 1930; Paradiso, 1969; Roberts and Early, 1952); *N. fuscipes* (Linsdale and Tevis, 1951); *N. fuscipes macrotis* Howel, 1926); *N. lepida lepida* (Barnes, 1922, 1927); *Papio cyncephalus* (Altman and Altman, 1970); *Perognathus parvus* (Johnson, 1961); *Peromyscus boylei* (Jameson, 1952); *P. leucopus* (Miller and Halls, 1969); *P. leucopus noveboracensis* (Hamilton, 1941b); *P. maniculatus* (Dalquest, 1948; Jameson, 1952; Miller and Halls, 1969; Schwartz and Schwartz, 1959; Walton, 1898); *P. maniculatus artemisiae* (Williams, 1959); *P. maniculatus bairdii* (Whitaker, 1966); *P. maniculatus gracilis* (Connor, 1960; Hamilton, 1941b); *P. maniculatus osgoodi* (Williams, 1959); *P. truei* (Bradford, 1974); Phascolomidae (Carter, Hill, and Tate, 1945); Peramelidae (Cleland, 1934); *Phenacomys intermedius mackenzii* (Harper, 1956); *Pitymys subterraneus* (Holišová, 1965); *P. tatricus* (Holišová, 1965); *Potorous tridactylus* (Brazenor, 1950); *P. tridactylus apicalis* (Guiler, 1971); Rodentia (Miller and Halls, 1969; Rolfe and Rolfe, 1925); Sciuridae (Brehm, 1895; Hamilton, 1939; Miller and Halls, 1969; Rolfe and Rolft, 1925); *Sciurus* spp. (Walker, 1964); *S. aberti aberti* (Bailey, 1931; Cahalane, 1947; MacClintock, 1970; Palmer, 1954; Patton, 1975; Seton, 1929; Stephenson, 1974); *S. carolinensis carolinensis* (Bailey, 1946; Ballou, 1927; Barber, 1954; Bernard, 1937; Burt, 1957; Cahalane, 1947; Cranbrook and Payn, 1962; Cross, 1942, 1946; Goodrum, 1940; Halls and Stransky, 1971; Hoffmeister and Mohr, 1957; Lyon, 1936; MacClintock, 1970; Martin *et al.,* 1951; Miller and Halls, 1969; Moore, 1943; Nelson, 1918; Palmer, 1954; Peterson, 1966; Robinson and Cowan, 1954; Schwartz and Schwartz, 1959; Shorten, 1962; Shorten and Courtier, 1955; Southern, 1964); *S. carolinensis hypophaeus* (Jackson, 1961; Larrison, 1970); *S. carolinensis pennsylvanicus* (Doutt, Heppenstall, and Guilday, 1967); *S. griseus griseus* (Cahalane, 1947; Miller and Halls, 1969; Sumner and Dixon, 1953); *S. kaibabensis* (Cahalane, 1947; Goldman, 1928; Hall, 1967; MacClintock, 1970; Nelson, 1918; Palmer, 1954); *S. niger cinerus* (Bailey, 1946); *S. niger niger* (Anthony and McSpadden, 1917; Allen, 1943; Barber, 1954; Baumgartner, 1939a, 1939b; Burt, 1957; Cahalane, 1947; Golley, 1962; Hall, 1955; Hoffmeister and Mohr, 1957; MacClintock, 1970; Matrin *et al.,* 1951; Moore, 1943; Palmer, 1954; Shafeldt, 1920); *S. niger rufiventer* (Larrison, 1970; Over and Churchill, 1941); *S. vulgaris* (Bourliere, 1956; Cranbrook and Payn, 1962; Lampio, 1967; Southern, 1964; Van Gelder, 1969); *S. vulgaris leucourus* (Shorten, 1959; 1962); *S. vulgaris orientis* (Abe, 1967); Soricidae (Martin *et al.,* 1951); *Spermophilus* spp. (Bourliere, 1956; Walker, 1964); *S. beecheyi* (Fitch, 1948; Linsdale, 1946); *S. lateralis chrysodeirus* (Bailey, 1936; Howell, 1938; Sumner and Dixon, 1953); *S. lateralis lateralis* (Bailey, 1931; Cahalane, 1947; Dalquest, 1948; Gordon, 1943; MacClintock, 1970; Seton, 1929); *S. richardsonii* (Hansen and Ueckert, 1970); *S. undulatus kennicottii* (Bee and Hall, 1956); *S. undulatus parryii* (Howell, 1938; Seton, 1971); *Spilogale* spp. (Howell, 1906); *S. putorius* (Bailey, 1946; Martin *et al.,* 1951); *Synaptomys cooperi cooperi* (Doutt, Heppenstall, and Guilday, 1967; Jackson, 1961; Martin *et al.,* 1951; Schwartz and Schwartz, 1959); *S. cooperi stonei* (Doutt, Heppenstall, and Guilday, 1967); Talpidae (Martin *et al.,* 1951; *Tamias* spp. Dalquest, 1948; Hamilton, 1939; Martin *et al.,* 1951); *T. striatus fisheri* (Bailey, 1946; Tunis, 1971); *T. striatus griseus* (Jackson, 1961); *T. striatus lysteri* (Allen, 1938; Doutt, Heppenstall, and Guilday, 1967; Gifford and Whitebread, 1951; Mearns, 1899; Seton, 1929); *T. striatus striatus* (Bailey, 1946; Cahalane, 1947; Golley, 1962; MacClintock, 1970; Schwartz and Schwartz, (1959); *Tamiasciurus* spp. (Bourliere, 1956; Palmer, 1954); *T. douglasi albolimbatus* (Bailey, 1936; Stevens, 1906); *T. douglasi douglasi* (Bailey, 1936; Broadbrooks, 1958; Cahalane, 1947; Dalquest, 1948; MacClintock, 1970; Nelson, 1918; Orr, 1949; Seton, 1929); *T. douglasi mollipilosus* (Bailey, 1936); *T. husonicus abieticola* (Golley, 1926); *T. hudsonicus dakotensis* (Over and Churchill, 1941); *T. hudsonicus fremonti* (Cahalane, 1947; Hatt, 1943; Olin, 1961); *T. hudsonicus hudsonicus* (Anthony and McSpadden, 1917; Burt, 1957; Cahalane, 1947; Cameron, 1956; Cram, 1924; Dalquest, 1948; Dice, 1921;

Hamilton, 1939; Jackson, 1931-1932; MacClintock, 1970; Marie, 1927; Martin *et al.*, 1951; Merriam, 1884; Murrill, 1902; Nelson, 1918; Peterson, 1966; Rand, 1948; Seagears, 1949, 1950; Seton, 1929; Van Gelder, 1969; Walton, 1903; Zim and Hoffmeister, 1955); *T. hudsonicus loquax* (Bailey, 1946; Connor, 1960; Doutt, Heppenstall, and Guilday, 1967; Grim and Roberts, 1950; Layne, 1954; Lyon, 1936; Paradiso, 1969; Roberts and Early, 1952); *T. hudsonicus lychnuchus* (Bailey, 1931); *T. hudsonicus minnesota* (Hamilton, 1943; Jackson, 1961; Over and Churchill, 1941); *T. hudsonicus mogollonensis* (Bailey, 1931); *T. hudsonicus preblei* (Harper, 1956); *T. hudsonicus richardsoni* (Bailey, 1936); *T. hudsonicus streatori* (Rust, 1946); *T. hudsonicus ventorum* (Barnes, 1922, 1927); *Vombatus hirsutus* (Brazenor, 1950).

Hypogoeus fungi, "truffles," hypogeous Gasteromycetes, basidiomycetous tubers, hypogeous Basidiomycetes, etc.

Apodemus sylvaticus (Watts, 1968); *Clethrionomys glareolus* (Watts, 1968); *Eutamias* spp. (Dowding, 1959); *E. amoenus* (Broadbrooks, 1958; Tevis, 1952); *E. quadrimaculatus* (Tevis, 1952, 1953); *E. townsendii* (Tevis, 1952, 1953); *Glaucomys sabrinus* (McKeever, 1960; Tevis, 1953); *Lepus europaeus* (Southern, 1964); Macropodidae (LeSouef and Burrell, 1926; Troughton, 1947); *Neotoma* spp. (Zeller, 1939); *N. cinerea* (Tevis, 1953); *Peromyscus boylei* (Tevis, 1953); *Phascolomys* spp. (LeSouef and Burrell, 1926); *Potorous* spp. (Troughton, 1943, 1944); Rodentia (Burnett, 1968; Gwynne-Vaughan, 1937); Sciuridae (Lohwag, 1932); *Sciurus griseus griseus* (Grinnel and Storer, 1924; Tevis, 1953); *Spermophilus* spp. (Dowding, 1959); *S. beecheyi* (Tevis, 1953); *Tamiasciurus douglasi douglasi* (Zeller, 1939).

Animals and the Fungi They Eat

CLASS MAMMALIA
ORDER MARSUPIALIA
Mesophellia spp.; *M. arenaria; Castoreum* spp.; *C. radicatum.*
FAMILY DIDELPHIDAE
Didelphis virginiana Kerr—opossum: *Coprinus* spp.; fungi.
FAMILY PERAMELIDAE
Mesophellia arenaria; fungi.
Isoden obesulus (Shaw)—short-nosed bandicoot: fungi.
FAMILY PHASCOLOMIDAE
Lycoperdales; fungi.
Phascolomys spp.: hypogeous fungi.
Vombatus hirsutus (Perry)—common wombat: fungi.
FAMILY MACROPODIDAE
Mesophellia arenaria; hypogeous fungi; fungi.
Potorous spp.: hypogeous fungi.
P. tridactylus Kerr—dark rat-kangaroo: fungi.
P. tridactylus apicalis (Gould): *Agaricus campestris; Oomycetales;* fungi.
ORDER INSECTIVORA
FAMILY SORICIDAE
Endogone spp.
Blarina spp.: *Glomus macrocarpus.*
B. brevicauda (Say)—short-tailed shrew: *Coprinus* spp.; *Endogone* spp.; *Glomus macrocarpus; Hymenogaster* spp.
Sorex spp.: fungi.
S. bendirii (Merriam)—Pacific water shrew: fungi.
S. cinereus Kerr—masked shrew: *Endogone* spp.; *Glomus macrocarpus.*
S. fumeus Miller—smoky shrew: *Endogone* spp.; *Glomus macrocarpus.*
S. pacificus: See *Sorex vagrans pacificus.*
S. trowbridgii Baird—Trowbridge's shrew: *Endogone* spp.
S. vagrans Baird—vagrant shrew: *Endogone* spp.
S. vagrans pacificus Coues: fungi.
S. vagrans yaquinae Jackson: *Endogone* spp.
S. yaquinae: see *Sorex vagrans yaquinae.*
FAMILY TALPIDAE
Endogone spp.; fungi.
ORDER PRIMATES
FAMILY CYNOPITHECINAE
Papio cynocephalus L.—yellow baboon: fungi.
ORDER ENDENTATA
FAMILY DASYPODIDAE
Dasypus novemcinctus mexicanus Peters—nine-banded armadillo: Lycoperdales, fungi.
D. novemcinctus texanus: See *Dasypus novemcinctus mexicanus.*
ORDER LAGOMORPHA
FAMILY LEPORIDAE

Amanita rubescens; Castoreum spp.; *Clitocybe brumadis; Elaphomyces granulatus; Hygrophoropsii aurantiaca; Melanogaster ambiguus; Mesophellia* spp.; *M. arenaria; M. pachythrix; Mycena epipterygia; Paxillus involutus; Polyporus betulinus; Sparassis crispa;* Tuberaceae; *Xerocomus badius.*

Lepus europaeus Pallus—brown hare: *Morchella* spp.; fungi.

Oryctolagus cuniculus (L.)—European rabbit: *Helvella* spp., *Lycoperdon* spp., *Marasmius* spp., *Scleroderma* spp.

Sylvilagus palustris paludicola (Miller and Bangs)—marsh rabbit: *Polyporus* spp.

FAMILY OCHOTONIDAE

Ochotona spp.: *Endogone* spp.

O. princeps (Richardson)—pika: *Endogone* spp.; *Glomus fasciculatus.*

ORDER RODENTIA

Amanita muscaria; Boletus edulis; Collybia maculata; Cortinarius collinitus; Elaphomyces granulatus; Hygrophoropsis aurantiaca; Hygrophorus hypothejus; Lactarius necator; L. rufus; Paxillus atrotomentosus; P. involutus; Russula emetica; Suillus bovinus; S. flavidus; S. variegatus; Tuber spp.; *T. aestivum; Xerocomus badius; X. chrysenteron;* fungi.

FAMILY SCIURIDAE

Amanita muscaria; Boletus spp.; *Cronartium ribicola; Elaphomyces granulatus; Hygrophorus pudorinus; Leccinum scabrum; Polyporus* spp.; *Tricholoma flavorvirens;* Tuberaceae.

Callospermophilus spp.: See *Spermophilus* spp.

Citellus spp.: See *Spermophilus* spp.

C. parryii parryii: See *Spermophilus undulatus parryii.*

C. richardsonii: See *Spermophilus richardsonii.*

Eutamias spp.; *Endogone* spp.; fungi.

E. amoenus (J. A. Allen)—yellow-pine chipmunk: Tuberales; hypogeous fungi.

E. cinereicollis cinereicollis (J. A. Allen)—gray-collored chipmunk: fungi.

E. minimus jacksoni: See *E. minimus neglectus.*

E. minimus neglectus (J. A. Allen)—least chipmunk: fungi.

E. minimus pictus (J. A. Allen): fungi.

E. quadrimaculatus (Gray)—long-eared chipmunk: *Boletus* spp.; *Clitocybe* spp.; Tuberales; hypogeous fungi; fungi.

E. quadrivittatus quadrivittatus (Say)—Colorado chipmunk: fungi.

E. speciosus (Merriam)—lodgepole chipmunk: fungi.

E. townsendii (Bachman)—Townsend's chipmunk: Tuberales, hypogeous fungi.

E. townseidii senex (J. A. Allen): fungi.

Glaucomys sabrinus (Shaw)—northern flying squirrel: hypogeous fungi; fungi.

G. sabrinus fuscus Miller: fungi.

G. sabrinus macrotis (Mearns): fungi.

G. volans volans (L.)—southern flying squirrel: fungi.

Pteromys volans: See *Glaucomys volans.*

Sciurus spp.: fungi.

S. aberti aberti Woodhouse—Abert's squirrel: *Agaricus* spp.; *Amanita muscaria; A. vaginata; Boletus* spp.; *Elaphomyces* spp.; *Gautieria* spp.; *Geopora cooperi; Glomus fasiculatus; Hysterangium* spp.; *Lepiota* spp.; *Lycoperdon* spp.; *Martellia* spp.; *Psathyrella* spp.; *Rhizopogon* spp.; *Russula* spp.; *Tuber* spp.; fungi.

S. carolinensis carolinensis Gmelin—eastern gray squirrel: Agaricaceae; *Amanita muscaria; Balsamia vulgaris; Boletus* spp.; *B. calopus; B. impolitus; Collybia maculata; Crepidotus malachias; Daedalea* spp.; *Dibotryon* spp.; *Elaphomyces granulatus; Flammulina velutipes; Hydnum erinaceus; Hygrocybe miniata; Hygrophorous hypothejus; Lactarius deliciosus; Leccinum scabrum; Lycoperdon* spp.; *Melanogaster ambiguus; Paxillus involutus; Pholiota discolor; Pleurotus ostreatus; Pluteus atricapillus; Polyporus* spp.; *P. picipes; P. sulphureus; Russula* spp.; *R. emetica; R. ochroleuca; Stereum hirsutum; Sullus bovinus; Tricholoma terreum;* fungi.

S. carolinensis hypophaeus Merriam: fungi.

S. carolinensis pennsylvanicus Ord.: fungi.

S. cinerus: See *S. carolinensis carolinensis.*

S. douglasii: See *Tamiasciurus douglasii.*

S. fremonti lychnuchus: See *Tamiasciurus hudsonicus lychnuchus.*

S. fremonti mogollonensis: See *Tamiasciurus hudsonicus mogollonensis.*

S. griseus griseus Ord—western gray squirrel: *Gautieria* spp.; *Hysterangium* spp.; *Melanogaster* spp.; Polyporaceae; *Rhizopogon* spp.; hypogeous fungi; fungi.

S. hudsonicus: See *Tamiasciurus hudsonicus hudsonicus.*

S. hudsonicus ventorum: See *Tamiasciurus hudsonicus ventorum.*

S. leucourus: See *Sciurus vulgaris leucourus.*

S. kaibabensis Merriam—Kaibab squirrel: fungi.

S. niger cinereus L.—eastern fox squirrel: fungi.

S. niger neglectus: See *S. niger cinereus.*

S. niger niger L.: Agaricaceae; *Boletus* spp.; *Crepidotus nephrodes; Flammulina velutipes; Hydnum erinaceus; Hygrocybe miniata; Lycoperdon gemmatum; Pholiota discolor; Pluteus atricapillus; Pleurotus* spp.; *P. ostreatus; Polyporus picipes; P. sulphureus;* fungi.

S. niger rufiventer E. Geoffroy St.-Hilaire: fungi.
S. vulgaris (L.)—European red or brown squirrel: *Agaricus campestris; Amanita* spp.; *Armillaria* spp.; *A. mella; Balsamia vulgaris; Boletus edulis; Cantharellus cibarius; Calocera viscosa; Kuehneromyces mutablis; Lactarius torminosus; Leccinum aurantiacum; L. scabrum; Naematoloma fasiculare; Polyporus betulinus; Suillus luteus; Xerocomus;* fungi.
S. vulgaris exalbidus Pallas: *Clitocybe* spp.; *Ganoderma* spp.; *Gomphidius glutinosus; Leccinum aurantiacum; L. scabrum; Pholiota* spp.; *Pluteus nanus; Suillus bovinus; S. luteus; S. piperatus; Xerocomus chrysenteron; X. subtomentosus.*
S. vulgaris leucourus Kerr.: Agaricales; fungi.
S. vulgaris orientis Thomas: fungi.
S. vulgaris varius: See *Sciurus vulgaris.*
Spermophilus spp.: Tuberales; hypogeous fungi; fungi.
S. beecheyi (Richardson)—California ground squirrel: hypogeous fungi; fungi.
S. lateralis (Say)—golden-mantled ground squirrel: *Polyporus* spp.; Tuberales; fungi.
S. lateralis chrysodeirus (Merriam): fungi.
S. richardsonii (Sabine)—Richardson's ground squirrel: fungi.
S. undulatus kennicottii (Ross)—arctic ground squirrel: fungi.
S. undulatus parryii (Richardson): fungi.
Tamias spp.; fungi.
T. striatus fisheri A. H. Howell—eastern chipmunk: Lycoperdaceae; fungi.
T. striatus griseus Mearns: *Geastrum* spp.; fungi.
T. striatus lysteri (Richardson): *Amanita vaginata; Russula* spp.; fungi.
T. striatus striatus (L.): fungi.
Tamiasciurus douglasi albolimbatus (J. A. Allen)—Douglas' squirrel: fungi.
T. douglasi cascadensis: See *T. douglasi mollipilosus.*
T. douglasi douglasi (Bachman): *Alpova diplophloeus; Boletus mirabilis; Gautieria graveolens; Gomphidius rutilus; G. subroseus; Pholiota lenta; Rhizopogon rubescens; R. vinicolor; Russula delica; Suillus granulatus; S. tomentosus; Truncocolumella citrina* var. *citrina;* Tuberales; fungi; hypogeous fungi.
T. douglasi mollipilosus (Aud. and Bachman): fungi.
T. fremonti: See *T. hudsonicus fremonti.*
T. hudsonicus abieticola (A. H. Howell)—red squirrel: fungi.
T. hudsonicus dakotensis (J. A. Allen): fungi.
T. hudsonicus fremonti (Aud. and Bachman): *Polyporus* spp.; *Russula* spp,. fungi.
T. hudsonicus hudsonicus (Erxleben): *Alpova diplophloeus; Amanita* spp.; *A. muscaria; A. phalloides; Amillaria mellea; Boletinus pictus; Boletus* spp.; *B. mirabilis; Cantharellus cibarius; Clitocybe* spp.; *C. brumalis; C. maxima; C. monodelpha; C. odora; Clavicorona pyxidata; Collybia dryophila; C. maculata; Cortinarius* spp.; *C. varius; Elaphomyces granulatus; Fomes fomentarius; F. pinicola; Gautieria graveolens; G. morchelliformis; Gomphidius rutilus; G. subroseus; G. tomentosus; Gomphus floccosus; Gymnopilus sapineus; Gyroporus castaneus; Hericium caput-ursi; Hydnum* spp.; *H. fuligineo-violaceum; H. imbricatum; H. repandum; Hygrophoropsis aurantiaca; Hygrophorus hypothejus; H. pudorinus; Hymenogaster tener; Inocybe* spp.; *Lactarius deliciosus; L. piperatus; L. uvidus; Leccinum scabrum; L. versipellis; Lentinus lepideus; Leucoagaricus naucinus; Lycoperdon pyriforme; Lyophyllum ulmarium; Melanogaster ambiguus; Morchella conica; M. esulenta; Naematoloma fasiculare; Oudemansiella radiacata; Paxillus involutus; Peridermium harknessii; Pholiota carbonaria; Pleurotus ostreatus; Polyporus* spp.; *P. amarus; P. betulinus; Psathyrella* spp.; *Ramaria aurea; R. flava; Rhizopogon luteolus; R. maculatus; R. occidentalis; R. roseolus; R. rubescens; R. viridis; R. vulgaris; Rozites caperata; Russula* spp.; *R. adusta; R. alutacea; R. bicolor; R. blackfordae; R. consobrina; R. decolorans; R. disparilis; R. emetica; R. emetica ssp. fragilis; R. mariae; R. nigricans; R. pulchella; R. rosea; R. rosipes; R. xerampelina; Suillus bovinus; S. cavipes; S. granulatus; S. lakei; S. luteus; S. subolivaceus; S. tomentosus; S. variegatus; Tricholoma* spp.; *T. flavovirens; Truncocolumella citrina;* Tuberales; fungi.
T. hudsonicus loquax (Bangs): *Lycoperdon* spp.; *Polyporus* spp.; fungi.
T. hudsonicus lychnuchus (Stone and Rehn): fungi.
T. hudsonicus minnesota (J. A. Allen): *Amanita* spp.; fungi.
T. hudsonicus mogollonensis (Mearns): fungi.
T. hudsonicus preblei A. H. Howell: fungi.
T. hudsonicus richardsoni (Bachman): fungi.
T. hudsonicus streatori (J. A. Allen): fungi.
T. hudsonicus ventorum (J. A. Allen): fungi.
FAMILY GEOMYIDAE
Tuber spp.
FAMILY HETEROMYIDAE
Dipodomys spp.—kangaroo rats: fungi.
Microdipodops spp.—kangaroo mice: fungi.
Perognathus parvus (Peale)—Great Basin pocket mouse: fungi.
FAMILY CASTORIDAE
Castor canadensis Kuhl—beaver: fungi.
FAMILY CRICETIDAE

Endogone spp.
Apodemus sylvaticus (L.)—wood-mouse: *Lycoperdon* spp.; *Paxillus involutus; Xerocomus badius;* fungi.
A. *flavicollis* Milch.—yellow-necked field mouse: fungi.
Clethrionomys spp.: *Glomus macrocarpus;* fungi.
C. californicus californicus (Merriam)—California red-backed vole: *Endogone flammicorona; E. lactiflua; E. pisiformis; Glomus fasiculatus; G. macrocarpus* var. *macrocarpus; G. microcarpus; G. monosporus; Sclerocystis rubiformis.*
C. gapperi athabascae (Preble)—Gapper's red-backed vole: fungi.
C. gapperi gapperi (Vigors): *Endogone* spp.; *Glomus macrocarpus; Hymenogaster* spp.; *Lactarius lignyotus;* fungi.
C. grapperi paludicola Doutt: fungi.
C. gapperi rhoadsii (Stone): fungi.
C. gapperi rupicola E. L. Poole: fungi.
C. glareolus Schreb.—European bank vole: *Balsamia* spp.; *Genea* spp.; *Hydnotrya* spp.; *Hymenogaster* spp.; *Melanogaster* spp.; *Rhizopogon spp.; Russula* spp.; *Tuber* spp.; fungi.
C. rufocanus Sund.—red-gray vole: fungi.
C. rutilus mikado Thomas—Emperor vole: Boletaceae Russulaceae.
Dicrostonyx groenlandicus (Traill)—Greenland varying lemming: fungi.
D. torquatus Pallas—collared lemming: fungi.
Lagurus curtatus (Cope)—sagebrush vole: *Endogone* spp.; *Glomus fasciculatus.*
Lemmiscus curtatus: See *Lagurus curtatus.*
Lemmus lemmus L.—Norwegian lemming: *Boletus* spp.; *Russula* spp.; fungi.
Microtus agrestis (L.)—North Europe dark vole: fungi.
M. chrotorrhinus (Miller)—rock vole: *Endogone* spp.
M. longicaudus (Merriam)—long-tailed vole: *Endogone* spp.
M. ochrogaster (Wagner)—prairie vole: *Endogone* spp.
M. oeconomus macfarlandi Merriam—tundra vole: *Endogone* spp.; *Hymenogaster* spp.
M. oregoni (Bachman)—Oregon meadow mouse: *Fischerula subcaulis.*
M. pennsylvanicus (Ord)—meadow vole: *Endogone* spp.; *Glomus fasciculatus; Melanogaster variegatus;* fungi.
M. pinetorum (Le Conte)—pine vole: *Endogone* spp.
Neotoma spp.: *Gautieria* spp.; Hymenogastrales; *Hysterangium* spp.; *Melanogaster* spp.; *Tuber rufum* var. *nitidum;* hypogeous fungi.
N. albigula warreni Merriam—white-throated wood rat: Lycoperdaceae.
N. cinerea (Ord)—bushy-tailed wood rat: *Lycoperdon* spp.; fungi; hypogeous fungi.
N. cinerea occidentalis Baird: *Lycoperdon* spp.; fungi.
N. cinerea orolestes Merriam: Agaricaeae; *Polyporus* spp.; fungi.
N. desertorum: See *N. lepida lepida.*
N. floridana attwateri Mearns—eastern wood rat: fungi.
N. floridana floridana (Ord): fungi.
N. floridana magister Baird: Agaricaceae; *Agaricus* spp.; *Boletus* spp.; *B. pallidus; Clavaria* spp.; *Inocybe* spp.; *Lycoperdon* spp.; *Russula* spp.; *Scleroderma citrinum;* fungi.
N. fuscipes annectens Elliot—dusky-footed wood rat: Agaricaceae; Boletaceae; *Elaphomyces* spp.; *Gautieria* spp.; *Hydnangium* spp.; Hymenogastrales; *Hymenogaster* spp.; *Hysterangium* spp.; *Melanogaster* spp.
N. fuscipes fuscipes Baird: *Helvella lacunosa; Melanogaster* spp.; *Morchella conica; Paxina acetabulum; Peziza* spp.; *P. emileia; Pluteus cervinus; Polyporus varius; Scleroderma hypogaeum; Tuber* spp.
N. fuscipes macrotis Thomas: fungi.
N. lepida lepida Thomas—desert wood rat: fungi.
N. magister: See *N. floridana magister.*
N. mexicana fallax Merriam—Mexican wood rat: fungi.
N. pennsylvanica: See *N. floridana magister.*
Onychomys leucogaster (Wied-Neuwied)—northern grasshopper mouse: *Endogone* spp.; *Glomus fasciculatus.*
Oryzomys palustris (Harlan)—marsh rice rat: *Endogone* spp.
Peromyscus spp.: *Glomus macrocarpus.*
P. boylii (Baird)—brush mouse: Tuberales; hypogeous fungi.
P. gossypinus (Le Conte)—cotton mouse: *Endogone* spp.
P. leucopus (Rafinesque)—white-footed mouse: *Endogone* spp.; Uredinales; fungi.
P. leucopus noveboracensis (Fisher): *Endogone* spp.; *Glomus macrocarpus;* fungi.
P. maniculatus (Wagner)—deer mouse: *Endogone* spp.; *E. flammicorona; E. lactiflua; E. pisiformis; Glomus caledonius; G. fasciculatus; G. macrocarpus; G. macrocarpus* var. *macrocarpus; G. microcarpus; Melanogaster variegatus; Sclerocystis rubiformis;* fungi.
P. maniculatus artemisiae (Rhoads): fungi.
P. maniculatus bairdii (Hoy and Kennicott); *Endogone* spp.; fungi.
P. maniculatus gracilis (Le Conte): *Endogone* spp.; fungi.
P. maniculatus osgoodi Mearns: fungi.
P. truei (Shufeldt)—piñon mouse: fungi.

Phenacomys intermedius Merriam—heather vole: *Endogone* spp.
P. intermedius mackenzii Preble: fungi.
P. ungava mackenzii: See *P. intermedius mackenzii.*
Pitymys pinetorum: See *Microtus pinetorum.*
P. subterraneus de Sél.-Long.—European ground vole: fungi.
P. tatricus Kratochvil—Tatra pine vole: fungi.
Synaptomys cooperi cooperi Baird—southern bog lemmings: *Endogone* spp.; *Glomus macrocarpus;* fungi.
S. cooperi gossii (Coues): *Endogone* spp.; *Glomus macrocarpus.*
S. cooperi stonei Rhoads: fungi.
FAMILY MURIDAE
Mastacomys spp.—broad-toothed rats: fungi.
Mus musculus L.—house mouse: *Endogone* spp.
FAMILY ZAPODIDAE
Napaeozapus insignis insignis (Miller)—woodland jumping mouse: *Endogone* spp.; *Hymenogaster* spp.; *Russula* spp.
Zapus hudsonius (Zimmermann)—meadow jumping mouse: *Endogone* spp.; *Hymenogaster* spp.
Z. princeps J. A. Allen—western jumping mouse: *Endogone* spp.; *Glomus fasiculatus; G. pulvinatus.*
Z. trinotatus Rhoads—pacific jumping mouse: *Endogone* spp.; *E. lactiflua; Glomus fasiculatus; G. monosporus; Sclerocystis rubiformis.*
ORDER CARNIVORA
FAMILY MUSTELIDAE
Spilogale spp.: fungi.
S. putorius (L.)—eastern spotted skunk: fungi.

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Literature Cited

Abe, H. 1967. Notes on the ecology of *Sciurus vulgaris orientis* Thomas. Mammal. Soc. Jap., J. 3: 118-124.
Allen, D. L. 1943. Michigan Fox Squirrel Management. Game Div. Dept. Conserv., Lansing, Mich. Game Div. Publ. 100. 404 pp.
Allen, E. G. 1938. The Habits and Life History of the Eastern Chipmunk, *Tamias striatus lysteri.* N.Y. St. Mus. Bull. 314. 122 pp.
Allen, J. M. 1952. Gray and fox squirrel management in Indiana. Ind. Dep. Conserv. Bull. 1. 112 pp.
Altman, S. A., and J. Altman. 1970. Baboon Ecology. Univ. Chicago Press, Chicago. 200 pp.
Andreotti, R. and U. Casoli. 1968. Composizione chimica e technologia di conservazione del tartufo. Industr. Conserve 43: 215-219.
Anthony, H. E., and J. W. Spadder (eds). 1917. Mammals of America. University Soc., N.Y. 335 pp.
Bailey, J. W. 1946. The Mammals of Virginia. Williams Printing Co., Richmond, Va. 416 pp.
Bailey, V. 1905. Biological Survey of Texas. N. Amer. Fauna 25. 222 pp.
————. 1931. Mammals of New Mexico. N. Amer. Fauna 53. 412 pp.
————. 1936. The Mammals and Life Zones of Oregon. N. Amer. Fauna 55. 416 pp.
Bakerspigel, A. 1956. *Endogone* in Saskatchewan rodents. Amer. J. Bot. 43: 471-475.
————. 1958. The spores of *Endogone* and *Melanogaster* in the digestive tracts of rodents. Mycologia 50: 440-442.
Ballou, W. H. 1927. Squirrels as mushroom eaters. J. Mammal. 8: 57-58.
Barber, H. L. 1954. Gray and fox squirrel food habit investigations. SE Assoc. Game Fish Comm. Proc. 8: 92-94.
Barger, N. R. 1947. The chipmunk. Wisc. Conserv. Bull. 12: 29-30.
Barkalow, F. S., Jr., and M. Shorten 1973. The World of the Grey Squirrel. J. B. Lippincott Co., N.Y. 160 pp.
Barnes, C T. 1922. Mammals of Utah. Univ. Utah, Bull. 12: 1-166.

————. 1927. Utah Mammals. Univ. Utah, Bull. 17: 1-183.
Barrett-Hamilton, G. E. H., and M. C. A. Hinton. 1921. A history of British mammals. Gurney & Jackson, London, 21: 696-720.
Baumgartner, L. L. 1939. Food of the fox squirrel in Ohio. Ohio Wildl. Res. Sta. Release 108. 7 pp. mimeo.
————. 1939 a. Foods of the fox squirrel in Ohio. N. Amer. Wildl. Conf., Trans. 4: 579-584.
Bee, J. W., and E. R. Hall. 1956. Mammals of Northern Alaska. Univ. of Kans. Mus. Natur. Hist. Misc. Publ. 8. 309 pp.
Benedict, R. G., V. E. Tyler, Jr., and L. R. Brady. 1967. Studies on spore germination and growth of some mycorrhizal-associated Basidiomycetes. Mycopath. Mycol. Appl. 31: 319-326.
Bergmann, W. 1953. The plant sterols. Ann. Rev. Plant Physiol. 4: 383-426.
Bernard, H. 1937. L'ecureuil gris. Soc. Can. d'Hist. Nat., Biblio Juenes Nat. tract 33: 1-4.
Bessey, E. A. 1935. Text-book of Mycology. P. Blakistan's Son & Co., Philadelphia. 495 pp.
Blair, W. F. 1936. The Florida marsh rabbit. J. Mammal. 17: 197-207.
Bourliere, F. 1956. The Natural History of Mammals. Second edition. (transl. from French by H. M. Parschley). Alfred A. Knopf, N.Y. 364 pp., xi.
Boyce, J. S. 1920. The dry-rot in incense cedar. U.S. Dep. Agr. Bur. Plant Ind. Bull. 871: 10.
Bradford, D. F. 1974. Water stress of free-living *Peromyscus truei*. Ecology 55: 1407-1414.
Brazenor, C. W. 1950. The Mammals of Victoria. Brown, Prior, Anderson Pty., Melbourne. 125 pp.
Brehm, A. E. 1895. Brehm's Life of Animals. Vol. I. Mammalia. A. N. Marquis & Co., Chicago. 616 pp.
Broadbrooks, H. E. 1958. Life history and ecology of the chipmunk, *Eutamias amoenus*, in eastern Washington. Univ. Mich. Mus. Zool. Misc. Publ. 103: 1-42.
Brown, L. G., and L. E. Yeager. 1945. Fox squirrels and grey squirrels in Illinois. Ill. Nat. Hist. Surv. Bull. 23: 449-536.
Buller, A. H. R. 1920. The red squirrel of North America as a mycophagist. Brit. Mycol. Soc. Trans. 6: 355-362.
————. 1922. The red squirrel of North America as a mycophagist. *In*: Researches on Fungi. Longmans, Green and Co., London. Vol. 2: 195-211.
Burdsall, H. H., Jr. 1968. A revision of the genus *Hydnocystis* (Tuberales) and of the hypogeous species of *Geopora* (Pezizales). Mycologia 60: 496-525.
Burnett, J. H. 1968. Fundamentals of Mycology. St. Martin's Press, N.Y. 546 pp.
Burt, W. H. 1928. Additional notes on the life history of the Goss lemming mouse. J. Mammal. 9: 212-216.
————. 1957. Mammals of the Great Lakes Region. Univ. Mich. Press, Ann Arbor. 246 pp.
Cahalane, V. H. 1942. Caching and recovery of food by the western fox squirrel. J. Wildl. Manage. 6: 338-352.
————. 1947. Mammals of North America. MacMillian Co., N.Y. 682 pp.
Calhoun, J. B. 1941. Distribution and food habits of mammals in the vicinity of the Reelfoot Lake Biological Station. Tenn. Acad. Sci. J. 16: 177-185, 207-225.
Cameron, A. W. 1956. A Guide to Eastern Canadian Mammals. Nat. Mus. Canada, Ottawa. 72 pp.
————. 1958. Canadian Mammals. Nat. Mus. Canada, Ottawa. 81 pp.
Carter, T. D., J. E. Hill, and G. H. Tate. 1945. Mammals of the Pacific World. MacMillan Co., N.Y. 227 pp.
Catalfomo, J., and J. M. Trappe. 1970. Ectomycorrhizal fungi: A phytochemical survey. Northw. Sci. 44: 19-24.
Ceruti, A., F. Montacchini, and C. Duployez. 1967. Ecologia dei funghi ipogei dell' "Arboretum Taurinense". Allionia 13: 89-105.
Chapman, F. B., and L. L. Baumgartner. 1939. Winter feeding of squirrels. Ohio Cons. Bull. 3: 6-7.
Christensen, C. M. 1951. The Molds and Man. Univ. Minnesota Press, Minneapolis. 284 pp.
Cleland, J. B. 1934, 1935. Toadstools and mushrooms and other larger fungi of South Australia. Adelaide; Government paper; Part I p. 1-178; Part II (1935) p. 179-362.
Cochrane, V. W. 1963. Physiology of fungi. John Wiley & Sons, N.Y. 524 pp.
Connor, P. F. 1953. Notes on the mammals of a New Jersey pine barrens area. J. Mammal. 34: 227-234.
————. 1960. The small mammals of Otsogo and Schoharie Counties. New York. N.Y. St. Mus. Bull. 382: 1-84.
Cooke, M. C. 1890. Animal mycophagists. Grevillea 19: 54.
Cooke, W. B. 1955. Fungi, lichens and mosses in relation to vascular plant communities in Eastern Washington and adjacent Idaho. Ecol. Monogr. 25: 119-180.
Corbet, G. B. 1966. The Terrestrial Mammals of Western Europe. G. T. Foulis & Co., London. 264 pp.
Cram, W. E. 1924. The red squirrel. J. Mammal. 5: 37-41.
Cranbrook, Earl of, and W. H. Payn. 1962. Squirrel survey. Suffolk Nat. Soc. Trans. 12: 184-185.
Cross, R. H., Jr. 1942. A Study of the Habits and Management of the Gray Squirrel in Virginia. Va. Polytech. Inst., Blacksburg, M. S. thesis. 40 pp.
————. 1946. The grey squirrel. Va. Wildl. 7: 14, 20.

Cunningham, G. H. 1942. The Gasteromycetes of Australia and New Zealand. John McIndee Printer, Dunedin. 236 pp.
Dalquest, W. W. 1948. Mammals of Washington. Univ. Kans. Publ. Mus. Nat. Hist. 2: 1-444.
Danilov, D. N. 1938. The caloric value of main food-stuffs of the squirrel. Zool. J., Moscow. 17: 734-738.
Dice, L. R. 1921. Notes on the mammals of interior Alaska. J. Mammal. 2: 20-28.
———. 1927. How do squirrels find buried nuts? J. Mammal. 8: 55.
Diehl, W. W. 1939. *Endogone* as animal food. Science 90: 442.
Doutt, J. K., C. A. Heppenstall, and J. E. Guilday. 1967. Mammals of Pennsylvania. Penn. Game Comm., Harrisburg. 281 pp.
Dowding, E. S. 1955. *Endogone* in Canadian rodents. Mycologia 47: 51-57.
———. 1959. Ecology of *Endogone*. Brit. Mycol. Soc. Trans. 42: 449-459.
Drożdź, A. 1966. Food habits and food supply of rodents in the beech forest. Acta Theriol. 11: 363-384.
Dudderar, G. R. 1967. A survey of the food habits of the gray squirrel *(Sciurus carolinensis)* in Montgomery County, Virginia. Va. Polytech. Inst., Blackburg, M.S. thesis. 72 pp.
Dunaeva, T., and V. Kucheruk. 1941. Material on the ecology of the terrestrial vertebrates of the tundra of south Yamal. Moscow Soc. Nat. Bull. 4: 1-80.
Du Reau, L. 1912. Parasitisme de *Balsamia vulgaris* (Vitt.) sur le Pin neir d'Autriche en Anjou. Soc. Sci. Nat. L'ouest France, Bull. Ser. 3. II: 39-42.
Endo, M. 1972. Plant sociological observations on the terrestrial larger fungi in an evergreen broad-leaved forest. (in Japanese). Jap. J. Ecol. 22: 51-61.
Finley, R. B., Jr. 1958. The wood rats of Colorado: distribution and ecology. Univ. Kans. Mus. Nat. Hist. Publ. 10: 213-552.
Fitch, H. S. 1948. Ecology of the California ground squirrel on grazing lands. Amer. Midl. Nat. 39: 513-596.
———, P. Goodrum, and C. Newman. 1952. The armadillo in the southeastern United States. J. Mammal. 33: 21-37.
Flake, L. D. 1971. An Ecological Study of Rodents in a Short-Grass Prairie of Northeastern Colorado. Grassland Biome, I.B.P., Tech. Rep. 100. 118 pp.
Fogel, F. 1976. Ecological studies of hypogeous fungi II. Sporocarp phenology in a western Oregon Douglas-fir stand. Can. J. Bot. 54: 1152-1162.
Ford, W. W. 1908. The pathology of *Amanita phalloides* intoxication. J. Infect. Dis. 5: 116-132.
———. 1910. The distribution of hemolysins, agglutinins and poisons in fungi, especially the amanitas, the entolomas, the lactarius and the inocybes. J. Pharm. Exp. Ther. 2: 285-318.
Fraleigh, L. B. 1929. Habits of mammals at an Adirondack camp. N.Y. St. Mus. Handb. 8: 119-153.
Fries, N. 1943. Untersuchungen über Sporenkeimung und Mycelentwicklung Bodenbewohnender Hymenomyceten. Symbol. Bot. Upsal. 6: 1-81.
Gäumann, E. A., and C. W. Dodge. 1928. Comparative Morphology of Fungi. McGraw-Hill Book Co., N.Y. 701 pp.
Gerdemann, J. W., and J. M. Trappe. 1974. The Endogonaceae in the Pacific Northwest. Mycol. Mem. No. 5. 76 pp.
Getz, L. L. 1968. Influence of water balance and microclimate on the local distribution of the redback vole and white-footed mouse. Ecology 49: 276-286.
Gifford, C. L., and R. Whitebread. 1951. Mammal Survey of South Central Pennsylvania. Penn. Game Comm., Harrisburg. 75 pp.
Goldman, E. A. 1928. The Kaibab or white-tailed squirrel. J. Mammal. 9: 127-129.
Golley, F. B. 1960. Energy dynamics of a food chain of an old-field community. Ecol. Monogr. 30: 187-206.
———. 1962. Mammals of Georgia. Univ. Georgia Press, Athens. 218 pp.
Goodrum, P. D. 1940. A population study of the gray squirrel in eastern Texas. Texas Agr. Exp. Sta. Bull. 591: 1-34.
Gordon, K. G. 1943. The natural history and behavior of the western chipmunk and mantled ground squirrel. Oreg. St. Monogr. Stud. Zool. 5: 7-38.
Grainger, J. 1946. Ecology of the larger fungi. Trans. Brit. Mycol. Soc. 29: 52-63.
Grim, W. C., and H. A. Roberts. 1950. Mammal Survey of Southwestern Pennsylvania. Penn. Game Comm., Harrisburg. 99 pp.
Grinnell, J., and T. I. Storer. 1924. Animal Life in the Yosemite. Univ. California Press, Berkeley. 752 pp.
Guiler, E. R. 1971. Food of the potoroo (Marsupialia, Macropodidae). J. Mammal. 52: 232-234.
Gwynne-Vaughan, H. C. I., and B. Barnes. 1937. The Structure and Development of the Fungi. Univ. Press, Cambridge. 449 pp.
Hall, E. R. 1955. Handbook of Mammals of Kansas. Univ. Kans. Mus. Nat. Hist. Misc. Publ. 7. 303 pp.
———, and K. R. Kelson. 1959. Mammals of North America. Ronald Press, N.Y. 2 vols.
Hall, J. G. 1967. White tails and yellow pines. Nat. Parks Mag. 41: 9-11.
Halls, L. K., and J. J. Stransky. 1971. Atlas of Southern Forest Game. South. Forest Exp. Sta., New Orleans. 24 pp.
Hamilton, W. J., Jr. 1930. The food of the Soricidae. J. Mammal. 11: 26-39.
———. 1939. American Mammals. McGraw-Hill Book Co., N.Y. 434 pp.

———. 1941. On the occurrence of *Synaptomys cooperi* in forested regions. J. Mammal. 21: 195.
———. 1941 a. Food of small forest mammals in eastern United States. J. Mammal. 21: 250-263.
———. 1943. The Mammals of Eastern United States. Comstock Publ. Co., N.Y. 432 pp.
———. 1958. Life history and economic relations of the opossum *(Didelphis marsupialis virginiana)* in New York State. N.Y. St. Coll. Agr. Mem. 354: 1-48.
Hansen, R. M., and P. N. Ueckert. 1970. Dietary similarity of some primary consumers. Ecology 51: 640-648.
Hansson, L. 1969. Spring populations of small mammals in central Swedish Lapland in 1964-68. Oikos 20: 431-450.
———. 1970. Methods of morphological diet micro-analysis in rodents. Oikos 21: 255-266.
———. 1971. Small rodent food, feeding and population dynamics. Oikos 22: 183-198.
Hardy, G. A. 1949. Squirrel cache of fungi. Can. Field Nat. 63: 86-87.
Harley, J. L. 1969. The Biology of Mycorrhizae. Leonard Hill, London. 334 pp.
———. 1971. Fungi in ecosystems. J. Ecol. 59: 653-668.
Harling, J., and M. McClaren. 1970. The occurrence of *Endogone macrocarpa* in stomachs of *Peromyscus maniculatus.* Syesis 3: 155-159.
Harper, F. 1956. The Mammals of Keewatin. Univ. Kans. Mus. Nat. Hist. Misc. Publ. 12. 94 pp.
Hastings, S., and J. C. Mottram. 1961. Observations upon the edibility of fungi for rodents. Brit. Mycol. Soc. Trans. 5: 364-378.
Hatt, R. T. 1929. The red squirrel: its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. Roosevelt Wild Life Annal 2: 7-146.
———. 1930. The biology of the voles of New York. Roosevelt Wild Life Bull. 5: 513-623.
———. 1943. The pine squirrel in Colorado. J. Mammal. 24: 311-345.
Hawker, L. E. 1954. British hypogeous fungi. Roy. Soc. (London) Phil. Trans. B. 237: 430-546.
Hering, T. F. 1966. The terricolous higher fungi of four Lake District woodlands. Brit. Mycol. Soc. Trans. 49: 369-383.
Hodgman, C. D., R. C. Weast, R. S. Shankland, and S. M. Selby. 1963. Handbook of Chemistry and Physics. Chemical Rubber Publ. Co., Cleveland. 3604 pp.
Hoffmeister, D. F., and C. O. Mohr. 1957. Fieldbook of Illinois Mammals. Ill. Nat. Hist. Survey Manual 4. 233 pp.
Holišová, V. 1960. Potrava myšice křovinné *Apodemus sylvaticus* L. no Českomoravské vrchovině. Zool. Listy 9: 135-158.
———. 1965. The food of *Pitymys subterraneus* and *P. tatricus* (Rodentia, Microtidae) in the mountain zone of the Sorbeto-Piceetum. Zool. Listy 14: 15-28.
———. 1971. The food of *Clethrionomys glareolus* at different population densities. Acta Sci. Nat. Brno 5: 1-34.
———. 1972. The food of *Clethrionomys glareolus* in a reed swamp. Zool. Listy 21: 293-307.
Howell, A. B. 1926. Anatomy of the Wood Rat. Baltimore, Williams and Wilkins Co. Mongr. Amer. Soc. Mammal. 1. 225 pp.
Howell, A. H. 1906. Revision of the skunks of the genus *Spilogale.* N. Amer. Fauna. 26: 1-55.
———. 1938. Revision of the North American ground squirrels with a classification of the North American Sciuridae. N. Amer. Fauna 56: 1-256.
Ingles, L. G. 1947. Mammals of California. Stanford Univ. Press, Stanford. 258 pp.
Ingold, C. T. 1953. Dispersal in Fungi. Clarendon Press, Oxford. 197 pp.
———. 1961. The Biology of Fungi. Hutchinson Educational, London. 144 pp.
———. 1966. Spore Release. *In:* Ainsworth, G. C., and A. S. Sussman, (eds.). The Fungi. Vol. 2: 679-707. John Wiley & Sons, N.Y. 805 pp.
———. 1973. The gift of a truffle. Brit. Mycol. Soc. Bull. 7: 32-33.
Jackson, H. H. T. 1928. A taxonomic review of the American long-tailed shrews (genera *Sorex* and *Microsorex*). N. Amer. Fauna 51: 1-238.
———. 1931-1932. The red squirrel, chatterer of the spruces. Home Geogr. Monthly 1-2: 19-24.
———. 1961. Mammals of Wisconsin. Univ. Wisconsin Press, Madison. 504 pp.
Jameson, E. W., Jr. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei,* in the northern Sierra Nevada, California. J. Mammal. 33: 50-60.
Johnson, D. R. 1961. The food habits of rodents on rangelands of southern Idaho. Ecology 42: 407-410.
Johnson, M. L., and B. T. Ostenson. 1959. Comments on the nomenclature of some mammals of the Pacific Northwest. J. Mammal. 40: 571-577.
———. 1968. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. Syst. Zool. 17: 23-30.
Kalmbach, E. R. 1944. The Armadillo in Its Relation to Agriculture and Game. Texas Game Fish and Oyster Comm. Bull. 60 pp.
Kavaler, L. 1965. Mushrooms, Molds, and Miracles. New American Library, N.Y. 256 pp.
Keith, J. O. 1965. The Abert squirrel and its dependence on ponderosa pine. Ecology 46: 150-163.
Kessler, K. J., Jr., and R. W. Blank. 1972. *Endogone* sporocorps associated with sugar maple. Mycologia 64: 634-638.
Klugh, A. B. 1927. Ecology of the red squirrel. J. Mammal. 8: 1-32.

Korf, R. P. 1973. Sparassoid ascocarps in Pezizales and Tuberales. Rep. Tottori Mycol. Inst., Japan 10: 389-403.
Krieger, L. C. C. 1967. The Mushroom Handbook. Dover Publ., N.Y. 560 pp.
Kumerloeve, H. 1956. Kännchen, *Oryctolagus cuniculus* (Linne, 1758) und Hasen, *Lepus europaeus* Pallas, 1778, als Pilzfresser. Saüg. Mitt. 4: 125-126.
Lamb, R. J., and B. N. Richards. 1974. Survival potential of sexual and asexual spores of ectomycorrhizal fungi. Brit. Mycol. Soc. Trans. 62: 181-191.
Lampio, T. 1967. Sex ratios and the factors contributing to them in the squirrel, *Sciurus vulgaris,* in Finland. Riistat. Julk. 29: 1-69.
Langham, C. L. 1916. Squirrel eating *Melanogaster ambiguus.* Irish Nat. 28: 136.
Larrison, E. J. 1970. Washington Mammals. Seattle Audubon Soc., Seattle. 243 pp.
Layne, J. N. 1954. The biology of the red squirrel *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. Ecol. Monogr. 24: 227-267.
Le Souef, A. S., and H. Barrell. 1926. The Wild Animals of Australasia. George C. Harrap and Co., London, 288 pp.
Lewis, D. H. 1973. Concepts in fungal nutrition and the origin of biotrophy. Biol. Rev. 48: 261-278.
Lilly, V. G., and H. L. Burnett. 1951. Physiology of the Fungi. McGraw-Hill Book Co., N.Y. 464 pp.
Linsdale, J. M. 1946. The California Ground Squirrel. Univ. California Press, Berkeley. 475 pp.
————, and L. P. Tevis, 1951. The Dusky-Footed Wood Rat. Univ. California Press, Berkeley. 664 pp.
Linzey, D. W., and A. V. Linzey. 1973. Notes on food of small mammals from Great Smoky Mountains National Park, Tennessee-North Carolina. J. Elisha Mitchell Sci. Soc. 89: 6-14.
Litten, W. 1975. The most poisonous mushrooms. Sci. Amer. 232: 91-101.
Lohwag, H. 1932. Über Truffelverkommen. Verhandl. Zool. Bot. Ges. Wien. 82: 117-123.
Lyon, M. W., Jr. 1936. Mammals of Indiana. Amer. Midl. Nat. 17: 1-384.
MacClintock, D. 1970. Squirrels of North America. Van Nostrand Reinhold Co., N.Y. 184 pp.
Marie, O. J. 1927. The Alaska red squirrel providing for winter. J. Mammal. 8: 37-40.
Marks, G. C., N. Ditchburne, and R. C. Foster. 1968. Quantitative estimates of mycorrhiza populations in radiata pine forests. Austral. For. 32: 26-38.
Marsden, W. 1964. The Lemming Year. Chatto and Windus, London. 252 pp.
Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American Wildlife and Plants: a Guide to Wildlife Food Habits. McGraw-Hill Book Co., N.Y. 500 pp.
Massee, G. 1911. British Fungi, with a Chapter on Lichens. George Routledge Sons, London. 551 pp.
McCorkindale, N. J., S. A. Hutchinson, B. A. Pursey, W. T. Scott, and R. Wheeler. 1969. A comparison of the types of sterol found in spores of the Saprolenginales and Leptomitales with those found in some other Phycomycetes. Phytochemistry 8: 861-867.
McKeever, S. 1960. Food of the northern flying squirrel in northeastern California. J. Mammal. 41: 270-271.
————. 1964. Food habits of the pine squirrel in northeastern California. J. Wildl. Manage. 28: 402-403.
Mearns, E. A. 1899. Mammals of the Catskill Mountains. U.S. Nat. Mus. Proc. 21: 352.
Mehrotra, B. S. 1967. The Fungi. Intern. Publ. House, Allahabad. 331 pp.
Melin, E., and H. Nilsson. 1957. Transport of C^{14} labelled photosynthate to the fungal associate of pine mycorrhiza. Svensk Bot. Tidskr. 51: 166-186.
Mendel, L. B. 1898. Chemical composition and nutritive value of some edible American fungi. Amer. J. Physiol. 1: 225-238.
Merriam, C. H. 1884. The vertebrates of the Adirondack region of northeastern New York. Linn. Soc. N.Y. Trans. 2: 1-214.
Metcalf, M. M. 1925. *Amanita muscaria* in Maine. Science, N. S. 61: 567.
Milazzo, F. H. 1965. Sterol production by some wood rotting Basidiomycetes. Can. J. Bot. 43: 1347-1353.
Miller, H. A., and L. K. Halls. 1969. Fleshy Fungi Commonly Eaten by Southern Wildlife. South. Forest Exp. Sta., New Orleans, La. 28 pp. (USDA Forest Serv. Res. Pap. SO-49.)
Miller, R. S. 1954. Food habits of the wood-mouse, *Apodemus sylvaticus* (Linne, 1758), and the bank vole, *Clethrionomys glareolus* (Schreber, 1780), in Wytham Woods, Berkshire. Saüg. Mitt. 2: 109-113.
Moffat, C. B. 1923. Food of the Irish squirrel. Irish Nat. 32: 77-82.
Moore, G. E. 1943. Food habits of squirrels. Mo. Conserv. 4: 14 (Dec.).
Murata, Y. 1976. Spores of higher fungi found in the stomach of *Clethrionomys rutilus mikado* Thomas, a kind of vole. [In Japanese.] Mycol. Soc. Jap., Trans. 17: 85-87.
Murrill, W. A. 1902. Animal mycophagists. Torreya 2: 25-26.
————. 1910. On fungi eaten by gray squirrels. Mycologia 2: 96.
Negus, N. C., E. Gould, and R. K. Chipman. 1961. Ecology of the rice rat, *Oryzomys palustris* (Harlow), on Breton Island, Gulf of Mexico, with a critique of the social stress theory. Tulane Stud. Zool. 8: 93-123.
Nelson, E. W. 1918. Wild animals of North America. National Geographic Soc., Washington, D.C. Pp. 385-612.

Newcombe, C. L. 1930. An ecological study of the Allegheny cliff rat (*Neotoma pennsylvanica* Stone). J. Mammal. 11: 204-211.
Nixon, C. M., D. M. Worley, and M. W. McClain. 1968. Food habits of squirrels in southeast Ohio. J. Wildl. Manage. 32: 294-305.
Odell, W. S. 1925. Squirrels eating *Amanita muscaria.* Can. Field Nat. 39: 180-181.
————————. 1926. Further observations on squirrels eating *Amanita.* Can. Field Nat. 40: 184.
Ognev, S. I. 1940-1950. Mammals of the USSR and adjacent countries. Vols. IV, V, VI, and VII. Transl. by Jean Salkind. Smithsonian Inst. and NSF, Washington, D.C.
Olin, G. 1961. Mammals of the Southwest Mountains and Mesas. Southw. Parks Monuments Assoc., Globe, Ariz. 126 pp.
Orr, R. T. 1949. Mammals of Lake Tahoe. Calif. Acad. Sci., San Francisco. 127 pp.
Over, W. H., and E. P. Churchill. 1941. Mammals of South Dakota. Mus. Dept. Zool., Univ. S. Dak., Vermillion. 56 pp.
Overholts, L. E. 1953. The Polyporaceae of the United States, Alaska, and Canada. Univ. Michigan Press, Ann Arbor. 466 pp.
Ovington, J. D. 1961. Some aspects of energy flow in plantations of *Pinus sylvestris* L. Ann. Bot., London N. S. 25: 12-20.
Packard, R. L. 1956. The Tree Squirrels of Kansas: Ecology and Economic Importance. Mus. Nat. Hist. St. Biol. Surv., Univ. Kans. Misc. Publ. 11: 67 pp.
Palenzona, M. 1969. Sintesi micorrizica tra *Tuber aestivum* Vitt., *Tuber brumale* Vitt., *Tuber melanosporum* Vitt. e semenzali di *Corylus avellana* L. Allionia 15: 121-132.
Palmer, R. S. 1954. The Mammal Guide. Doubleday and Co., Garden City, N.Y. 384 pp.
Paradiso, J. L. 1969. Mammals of Maryland. N. Amer. Fauna 66. 193 pp.
Parks, H .E. 1919. Notes on California fungi. Mycologia 11: 15-20.
————————. 1921. Californian hypogeous fungi. Tuberaceae. Mycologia 13: 301-314.
————————. 1922. The genus *Neotoma* in the Santa Cruz Mountains. J. Mammal. 3: 241-253.
Patton, D. R. 1975. Abert Squirrel Cover Requirements in Southwestern Ponderosa Pine. USDA, Forest Serv., Rocky Mt. Forest Range Exp. Sta. Res. Pap. RM-145. 12 pp.
Peterson, R. L. 1966. The Mammals of Eastern Canada. Oxford Univ. Press, Toronto. 465 pp.
Pilát, A., and O. Usak. 1958. Mushrooms. Spring Books, London. 340 pp.
Poole, E. L. 1940. A life history sketch of the Allegheny wood rat. J. Mammal. 21: 249-270.
Proudfit, F. T., and C. H. Robinson. 1961. Normal and Therapeutic Nutrition. MacMillan, N.Y. 858 pp.
Rainey, D. G. 1956. Eastern woodrat, *Neotoma floridana*: life history and ecology. Univ. Kans. Mus. Nat. Hist. Publ. 8: 535-646.
Rajala, P., and T. Lampio. 1963. The food of the squirrel *(Sciurus vulgaris)* in Finland in 1945-1961. Soumen Riista, Helsinki 16: 155-185.
Rand, A. L. 1948. Mammals of the Eastern Rockies and Western Plains of Canada. Nat. Mus. Can. Bull. 108. 237 pp.
Reess, M., and C. Fisch. 1887. Untersuchungen unter Bau und Lebengeschichte der Hirschtrüffel, *Elaphomyces.* Bibl. Bot. 7: 1-24.
Richardson, M. J. 1970. Studies on *Russula emetica* and other agarics in a Scots pine plantation. Brit. Mycol. Soc. Trans. 55: 217-229.
Roberts, H. A., and R. C. Early. 1952. Mammal Survey of Southeastern Pennsylvania. Penn. Game Comm., Harrisburg. 70 pp.
Robinson, D. J., and I. McT. Cowan. 1954. An introduced population of the gray squirrel *(Sciurus carolinensis gmelin)* in British Columbia. Can. J. Zool. 32: 261-282.
Rolfe, R. T., and F. W. Rolfe. 1925. The Romance of the Fungus World. Chapman and Hall Ltd., London. 309 pp.
Rue, L. L. 1967. Pictorial Guide to the Mammals of North America. Thos. Y. Crowell Co., N.Y. 299 pp.
Rust, H. J. 1946. Mammals of northern Idaho. J. Mammal. 27: 308-327.
Schmidt, F. J. W. 1931. Mammals of western Clark County, Wisconsin. J. Mammal. 12: 99-117.
Schwartz, C. W., and E. R. Schwartz. 1959. The Wild Mammals of Missouri. Univ. Missouri Press, Kansas City. 341 pp.
Seagears, C. 1949-1950. The red squirrel. N.Y. St. Conserv. 4: 40-44 (Dec.).
Seton, E. T. 1909. Life-Histories of Northern Animals. Charles Scribner's Sons, N.Y. Vol. 1.
————————. 1911. The Arctic Prairies. Charles Scribner's Sons, N.Y. 415 pp.
————————. 1929. Lives of Game Animals. Doubleday, Doran and Co., N.Y. 4: 1-440.
Sheldon, C. 1934. Studies on the life histories of *Zapus* and *Napaeozapus* in Nova Scotia. J. Mammal. 15: 290-300.
————————. 1936. The mammals of Lake Kedgemakooge and vicinity, Nova Scotia. J. Mammal. 17: 207-215.
Shemakhanova, N. M. 1967. Mycotrophy of Woody Plants. Israel Prog. Sci. Transl., Jerusalem, U.S. Dep. Commerce TT 66-51073. 329 pp.
Shivrina, A. N., E. G. Platonova, and Y. P. Cherotchenko. 1968. Higher Basidiomycetes as sources of ergosterol. Mikol. Fitopatol. 2: 65-69.
Shorten, M. 1959. Squirrels in Britain. *In*: Flyger, V. (ed.) Symposium on the Gray Squirrel. Chesapeake Biol. Lab., Contrib., Salamono, Md. Pp. 375-378.
————————. 1962. Squirrels; Their Biology and Control. H. M. Stationary Off., London. 44 pp.

————, and F. A. Courtier. 1955. A population study of the grey squirrel *(Sciurus carolinensis)* in May 1954. Ann. Appl. Biol. 43: 494-510.
Shufeldt, R. W. 1920. Four-footed foresters—the squirrels. Amer. For. 26: 37-44.
Singer, R. 1961. Mushrooms and Truffles. Interscience Publ., N.Y. 269 pp.
————. 1962. The Agaricales in Modern Taxonomy. J. Cramer, Weinheim. 915 pp.
Smith, A. H. 1949. Mushrooms in Their Natural Habitats. Sawyer's Inc., Portland, Or. 626 pp.
————. 1951. Puffballs and Their Allies in Michigan. Univ. Michigan Press, Ann Arbor. 131 pp.
————. 1965. New and unusual Basidiomycetes with comments on hyphal and spore wall reactions with Melzer's solution. Mycopathol. Mycol. Appl. 26: 385-402.
Smith, C. C. 1965. Interspecific competition in the genus of tree squirrels *Tamiasciurus*. Univ. Wash., Seattle. Ph.D. thesis. 269 pp.
————. 1970. The coevolution of pine squirrels *(Tamiasciurus)* and conifers. Ecol. Monogr. 40: 349-371.
Smith, G. M. 1938. Cryptogamic Botany. McGraw-Hill Book Co., N.Y. Vol. 1. 545 pp.
Smith, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. J. Wldl. Manage. 32: 305-317.
Southern, H. N. (ed.). 1964. The Handbook of British Mammals. Blackwell Sci. Publ., Oxford. 465 pp.
Spaulding, P. 1922. Investigations of the white-pine blister rust. U.S. Dep. Agr. Bur. Plant Ind. Bull. 957: 35-36.
Stakhrovskii, V. C. 1932. The biology of squirrels kept in open air cages. (In Russian.) Zool. Zh. 11: 82-104.
Stark, N. 1972. Nutrient cycling pathways and litter fungi. Bioscience 22: 355-360.
Stephens, F. 1906. California Mammals. West Coast Publ. Co., San Diego, Calif. 351 pp.
Stephenson, R. L. 1974. Seasonal food habits of Abert's squirrels *Sciurus aberti*. J. Ariz. Acad. Sci. 9(suppl.): 8.
————. 1975. Reproductive Biology and Food Habits of Abert's Squirrels in Central Arizona. Arigona State Univ., M. S. thesis. 66 pp.
Stienecker, W., and B. M. Browning. 1970. Food habits of the western gray squirrel. Calif. Fish Game. 56: 36-48.
Stoner, D. 1918. The Rodents of Iowa. Iowa Geol. Surv. Bull. 5. 172 pp.
Styan, K. E. 1946. Squirrel with a toadstool. Field, London 187: 49 (letter).
Sumner, L., and J. S. Dixon. 1953. Birds and Mammals of the Sierra Nevada. Univ. California Press, Los Angeles. 484 pp.
Sussman, A. S., and H. O. Halvorson. 1966. Spores: Their Dormancy and Germination. Harper and Row, N.Y. 354 pp.
Taylor, W. P. 1920. The wood rat as collector. J. mammal. 1: 91-92.
Tevis, L. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. J. Mammal. 33: 198-205.
————. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. J. Mammal. 34: 316-324.
Thaxter, R. 1922. A revision of the Endogonaceae. Amer. Acad. Arts Sci., Proc. 57: 291-341.
Theodorou, C., and G. D. Browen. 1973. Inoculation of seeds and soil with basidiospores of mycorrhizal fungi. Soil Biol. Biochem. 5: 765-771.
Trappe, J. M. 1962. Fungus associates of ectotrophic mycorrhizae. Bot. Rev. 28: 538-606.
————. 1971. Mycorrhiza-forming Ascomycetes. *In*: Hacskaylo, E. (ed.), Mycorrhizae. U.S. Dep. Agric., Misc. Publ. 1189: 19-37.
————. 1971a. A synopsis of the Carbomycetaceae and Terfeziaceae (Tuberales). Brit. Mycol. Soc. Trans. 57: 85-92.
————. 1975. The genus *Fischerula* (Tuberales). Mycologia 67: 934-941.
————, and C. Maser. 1976. Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. Mycologia 68: 433-436.
Troughton, E. 1943. The kangaroo family. Rat kangaroos, I. Austl. Mus. Mag. 8: 171-175.
————. 1944. The kangaroo family. Hare wallabies. Austl. Mus. Mag. 8: 229-233.
————. 1947. Furred Animals of Australia. Charles Scribner's Sons, N. Y. 374 pp.
Tunis, E. 1971. Chipmunks on the Doorstep. Thos. Y. Crowell Co., N.Y. 70 pp.
Uhlig, H. C. 1955. The Gray Squirrel: Its Life History, Ecology, and Population Characteristics in West Virginia. W. Va. Conserv. Comm. 175 pp.
VanGelder, R. G. 1969. Biology of Mammals. Charles Scribner's Sons, N.Y. 197 pp.
Walker, E. P. 1964. Mammals of the World. Johns Hopkins Press, Baltimore, Maryland. Vol. 2. 1500 pp.
Walton, M. A. 1898. The red squirrel. Forest Stream. P. 43.
————. 1903. A hermit's wild friends. D. Estes and Co., Boston. 304 pp.
Warren, E. R. 1920. Notes on wood rat work. J. Mammal. 1: 233-235.
————. 1942. The Mammals of Colorado, Second Edition. Univ. Oklahoma Press, Norman. 330 pp.
Watson, A. 1956. Ecological notes on the lemmings *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* in Baffin Island. J. Animal Ecol. 25: 289-302.

Watts, C. H. S. 1968. The foods eaten by woodmice (*Apodemus sylvaticus* and bank voles *(Clethrionomys glareolus)* in Wytham Woods, Berkshire. J. Anim. Ecol. 37: 25-41.
Whitaker, J. O., Jr. 1962. *Endogone, Hymenogaster,* and *Melanogaster* as small mammal foods. Amer. Midl. Nat. 67: 152-156.
————. 1963. Food, habitat and parasites of the woodland jumping mouse in central New York. J. Mammal. 44: 316-321.
————. 1963 a. Food of 120 *Peromyscus leucopus* from Ithaca, New York. J. Mammal. 44: 418-419.
————. 1966. Food of *Mus musculus, Peromyscus maniculatus bairdi* and *Peromyscus leucopus* in Vigo County, Indiana. J. Mammal. 47: 473-486.
————, and M. G. Ferraro. 1963. Summer food of 220 short-tailed shrews from Ithaca, New York. J. Mammal. 44: 419.
————, and C. Maser. 1976. Food habits of five Western Orgeon shrews. Northw. Sci. 50: 102-107.
Wilkins, W. H., and G. C. Harris. 1946. The ecology of the larger fungi. V. An investigation into the influence of rainfall and temperature on the seasonal production of fungi in a beechwood and a pinewood. Ann. Appl. Biol. 33: 179-188.
Williams, O. 1959. Food habits of the deer mouse. J. Mammal. 40: 415-419.
————, and B. A. Finney. 1964. *Endogone*—food for mice. J. Mammal. 45: 265-271.
Winton, A. L., and K. B. Winton. 1932. The Structure and Composition of Foods. John Wiley and Sons, N.Y. Vol. I. 710 pp.
————, and ————. 1935. The Structure and Composition of Foods. John Wiley and Sons, N.Y. Vol. II. 904 pp.
Zeller, S. M. 1939. Developmental Morphology of *Alpova.* Oreg. St. Monog., Stud. Bot. 2. 19 pp.
Zemanek, M. 1972. Food and feeding habits of rodents in a deciduous forest. Acta Theriol. 17: 315-325.
Zim, H. S., and D. F. Hoffmeister. 1955. Mammals. Simon and Schuster, N.Y. 160 pp.
Zimmerman, E. G. 1965. A comparison of habitat and food of two species of *Microtus.* J. Mammal. 46: 605-612.
————. 1965a. A comparison of food habits of two species of *Microtus.* Ind. Acad. Sci. Proc. 75: 281.

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Unusual Occurrence of Pink Salmon (Oncorhynchus gorbuscha) in the Snake River of Southeastern Washington

Abstract

The first positively identified adult pink salmon *(Oncorhynchus gorbuscha)* is reported for the Snake River of Southeastern Washington State. The sightings were in the Tucannon River and at Little Goose and Lower Granite Dams, approximately 625 to 694 km from the Pacific Ocean. Spent female pink salmon carcasses indicated that these fish can migrate long distances and arrive in time to spawn.

Pink salmon *(Oncorhynchus gorbuscha)* of northwestern North America commonly spawn in relatively short coastal streams. In large rivers, they seldom penetrate more than 160 km upstream to spawn (Aro and Shepard, 1967; Atkinson, Rose, and Duncan, 1967; and McPhail and Lindsey, 1970). Neave (1966), however, reported that a substantial segment of the Fraser River pink salmon run travels at least as far upstream as the South Thompson River, about 560 km from the sea.

During the fall of 1975 we observed pink salmon at several locations on the Snake River (a major tributary of the Columbia River) in southeastern Washington State. The most upstream observation was made at river kilometer 694 (Lower Granite Dam), measured from the mouth of the Columbia River.

Although we believe these to be the first sightings of pink salmon in the Snake River drainage, pinks have been counted in the fish ladder at Bonneville Dam on the lower Columbia River as early as 1941 (personal communication with Mr. Ray Oliger, U.S. Army Corps of Engineers, Walla Walla, Washington). At most dams on the Columbia and Snake Rivers, counting stations are operated at some point on the fishway. Salmonids pass over a "counting board" and the counter identifies and tallies a fish instantaneously. Since pink salmon are rare upstream from Bonneville Dam, fish counters are not expected to recognize an incidental run. Therefore, when a pink escapement larger than expected occurred in 1975, some dam counts showed pinks, whereas others did not. Probably the total run was greater than recorded. At any rate, counts in 1975 were: Bonneville Dam—309; The Dalles Dam—0; John Day Dam—45; McNary Dam —0; Ice Harbor Dam—0; Lower Monumental Dam—0; Little Goose Dam—12; and Lower Granite Dam—0. We made an independent observation at Lower Granite Dam (one fish).

The National Marine Fisheries Service (NMFS) operates trapping facilities for adult salmon and steelhead trout *(Salmo gairdneri)* at Little Goose and Lower Granite

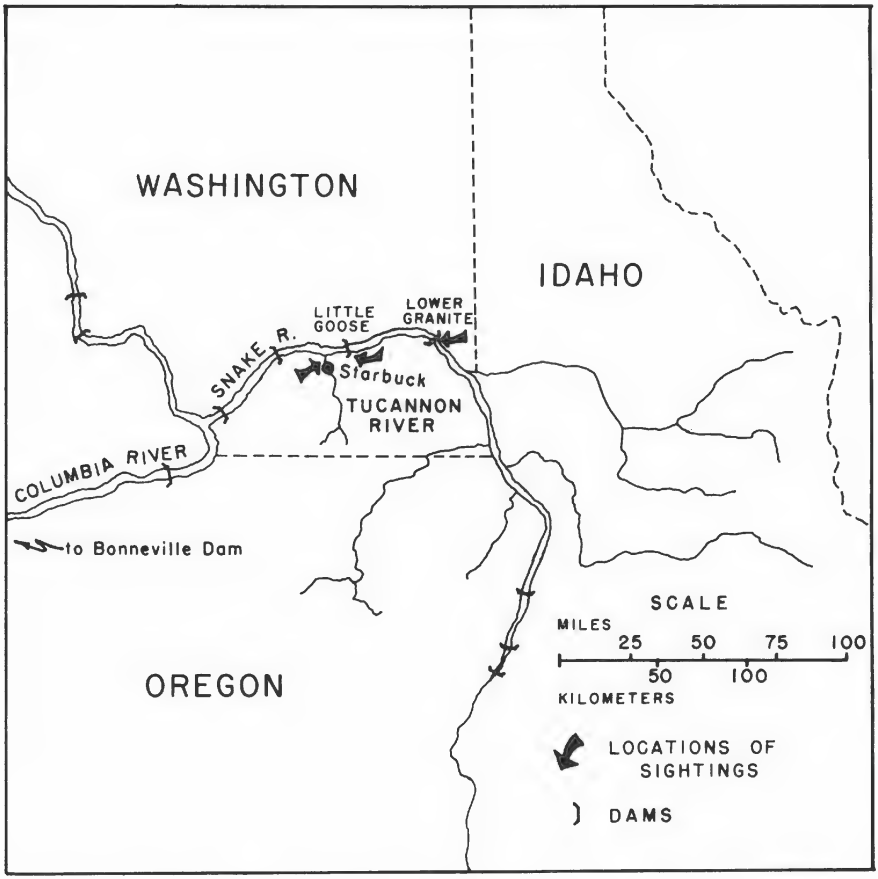

Figure 1. The lower Snake River and locations where pink salmon were observed.

Dams on the lower Snake River (Fig. 1). On September 24, 1975, a male pink salmon 559 mm long weighing 1.6 kg was captured at Little Goose Dam. The external characteristics we used for identification included: a large hump with a very thin keel; extremely small scales; spots on both lobes of the caudal fin, spots larger than the pupil of the eye; yellow and pink coloration below the lateral line. In early October, a female pink salmon was captured at Little Goose Dam and a male pink salmon was captured at Lower Granite Dam 60 km upstream of Little Goose Dam.

During the fall of 1975, routine spawning ground surveys were made for fall chinook salmon *(Oncorhynchus tshawytscha)* spawning in the lower Tucannon River, a small tributary of the Snake River near Starbuck, Washington (about 625 km from the Pacific Ocean). Five pink salmon carcasses were recovered on these surveys: one on October 18, three on October 25, and one on November 1. One of the carcasses was sent to Dr. Richard L. Wallace, Associate Professor of Zoology at the University of Idaho, for species verification. He determined that it was a spent female pink salmon

573 mm in length. The following characters were used in the identification: gill rakers—12 upper and 19 lower; pored scales in lateral line—167; scales in first row above lateral line—203; pyloric caeca—173. This specimen was added to the collection of the Department of Biological Sciences at the University of Idaho.

The four carcasses of female pink salmon recovered from the lower Tucannon River contained only a few eggs and their caudal fins were frayed as if from redd building. Although the redds we observed could not be positively identified as those of pink salmon (spawning fall chinook salmon were present), the observations indicate that pink salmon can reach the lower Snake River area in time and in condition to spawn successfully.

Contacts with fishery agencies of Washington, Oregon, and Idaho have revealed no known attempts to establish pink salmon in the Snake River drainage. The fish may be remnants of a small Columbia River stock which may now be entering the Snake River system. It is unlikely that they are strays from a short-run costal stock. However, they could be strays from long-run stocks such as those from the Frazier River system.

Literature Cited

Aro, K., and M. Shepard. 1967. Salmon of the North Pacific Ocean—part IV: Spawning populations of North Pacific salmon. 5. Pacific salmon in Canada. Int. North Pac. Fish. Comm., Bull. 23:225-327.

Atkinson, C., J. Rose, and T. Duncan. 1967. Salmon of the North Pacific Ocean—part IV: Spawning populations of North Pacific salmon. 4. Pacific salmon in the United States. Inst. North Pac. Fish. Comm., Bull. 23:43-223.

McPhail, J., and C. Linsey. 1970. Freshwater Fishes of Northwestern Canada and Alaska. Fish. Res. Bd. Canada, Bull. 173. 381 pp.

Neave, F. 1966. Salmon of the North Pacific Ocean—part III: A review of the life history of North Pacific salmon. 5. Pink salmon in British Columbia. Int. North Pac. Fish. Comm., Bull. 18: 71-79.

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Plant Ecology and Natural History of Chowder Ridge, Mt. Baker: A Potential Alpine Research Natural Area in the Western North Cascades

Abstract

The natural history of Chowder Ridge is of particular interest for several reasons: (1) Chowder Ridge contains the largest area of continuous alpine vegetation in the western North Cascades. The area is especially impressive if considered jointly with the adjacent northwest-southeast section of Skyline Divide. (2) Because of the southwest aspect of Chowder Ridge, water stresses are more critical than those typifying the North Cascades in general. This fact results in a curious mixture of relatively drought-tolerant plants more frequently encountered in the eastern Cascades and Rocky Mountains with the characteristic species of the western North Cascades. (3) Chowder Ridge contains all the landforms characteristically associated with the alpine zone, e.g., frost heaving, rock stripes, soil stripes, vegetation stripes, turf-banked terraces, turf-banked lobes, massive solifluction, coarse talus, extensive fell-fields, and sparsely vegetated rock formations. (4) Chowder Ridge is of sedimentary origin whereas associated mountain formations are composed primarily of andesite. (5) Chowder Ridge remains more or less undisturbed by man; thus the flora and fauna have remained in a relatively natural state. Because of this unique combination of physical and biological characteristics, the Chowder Ridge area is incomparably suited for Research Natural Area designation.

Introduction

Until the recent work of Douglas (1971, 1972, 1973) and Douglas and Bliss (1977), botanical studies in the North Cascades in general and the Mt. Baker area in particular were restricted in number and limited in scope, including floristic descriptions (Gorman, 1907; St. John and Hardin, 1929; Muenscher, 1941; Douglas and Taylor, 1970; Taylor *et al.,* 1973) and regional community analyses (Franklin and Dyrness, 1969; Franklin and Trappe, 1963). However, with the work of Douglas (especially 1973) and extensive collecting by the authors, it is now possible to evaluate the Chowder Ridge area (including the adjacent northwest-southeast section of Skyline Divide) with respect to other alpine areas in the western North Cascades. From this evaluation, we are convinced that the Chowder Ridge area should be incorporated into the Research Natural Area (RNA) system of the Pacific Northwest as the principal alpine representative of the western North Cascades. At the present time there is no representation of an "alpine community mosaic with krummholz tree groups" in the western North Cascades (Dyrness *et al.,* 1975). The Chowder Ridge area is the ideal candidate to fill this need.

Research Natural Areas are natural ecological reserves which were defined by Dyrness *et al.* (1975) as "naturally occurring physical or biological units where natural conditions are maintained insofar as possible." The Federal Committee on Research Natural Areas (1968) described the objectives of the RNA system as follows: (1) preservation of examples of all significant natural ecosystems for comparison with those influenced by man; (2) provision of educational and research areas for ecological and environmental studies; (3) preservation of gene pools for typical and rare and endangered plants and animals. A fourth very important objective would seem to be the study of evolutionary processes, especially unique adaptations of plants and animals. This justification for establishment of RNAs in addition to national parks, wilderness areas, etc., is that the latter land-use classification types are dedicated to conservation and/or recreation, not research and education. It is fortunate that the Chowder Ridge area occurs within the Mt. Baker National Forest inasmuch as the forest service is dedicated to the RNA system and has established a major objective of representing as many of the natural plant community types as possible (Romancier, 1974).

Description of the Chowder Ridge Area

Chowder Ridge is located in the Mt. Baker National Forest, within Township 38N and Range 7E. The ridge crest is approximately 5 km long and is oriented from northwest, as a continuation of Skyline Divide, to southeast, running into Bastile Ridge and Mazama Glacier of Mt. Baker (Fig. 1). Elevation varies from 2,031 m (just above Skyline Divide) to 2,312 m at the highest point, with a mean approximately 2,154 m. Both the southwest and northeast slopes are steep (approximately 45 percent), the latter being covered by late-melting snow or ice fields.

The weather of Chowder Ridge is variable and often severe. The prevailing winds follow the general pattern for that of the North Cascades, northwesterly during spring and summer and southwesterly during fall and winter (Douglas, 1972). The nearest meteorological data are recorded from the Mt. Baker station (1,296 m). At that site, the mean annual precipitation is 2,790 mm with only 274 mm occurring during the summer months (June, July, and August). The mean annual temperature is 4.4C with a July mean of 12.1C.

Geologic History

The Mt. Baker area is characterized by landforms caused by sedimentation, uplift, volcanics, and glaciation. The oldest rocks in the area belong to the Yellow Aster complex. Basement rocks are made up of the Shuksan Group metamorphics, Chilliwack Group sediments and volcanics, and the Nooksack Group sediments (Easterbrook and Rahm, 1970). Mt. Baker itself is a composite volcano made of alternating layers of lava and pyroclastic materials.

The ruggedness of the area is due in large part to the action of alpine glaciers which reached their maximum development during the Pleistocene Ice Age and again as recently as 500 years ago. Alpine glaciers were overrun below about 1,700 m by continental ice sheets, the last (Fraser Glaciation) receding 10,000 years ago (Easterbrook and Rahm, 1970). At present the alpine glaciers fluctuate in size as a consequence of temperature variations and snow accumulation.

According to Misch (1966), most of Chowder Ridge is of sedimentary origin,

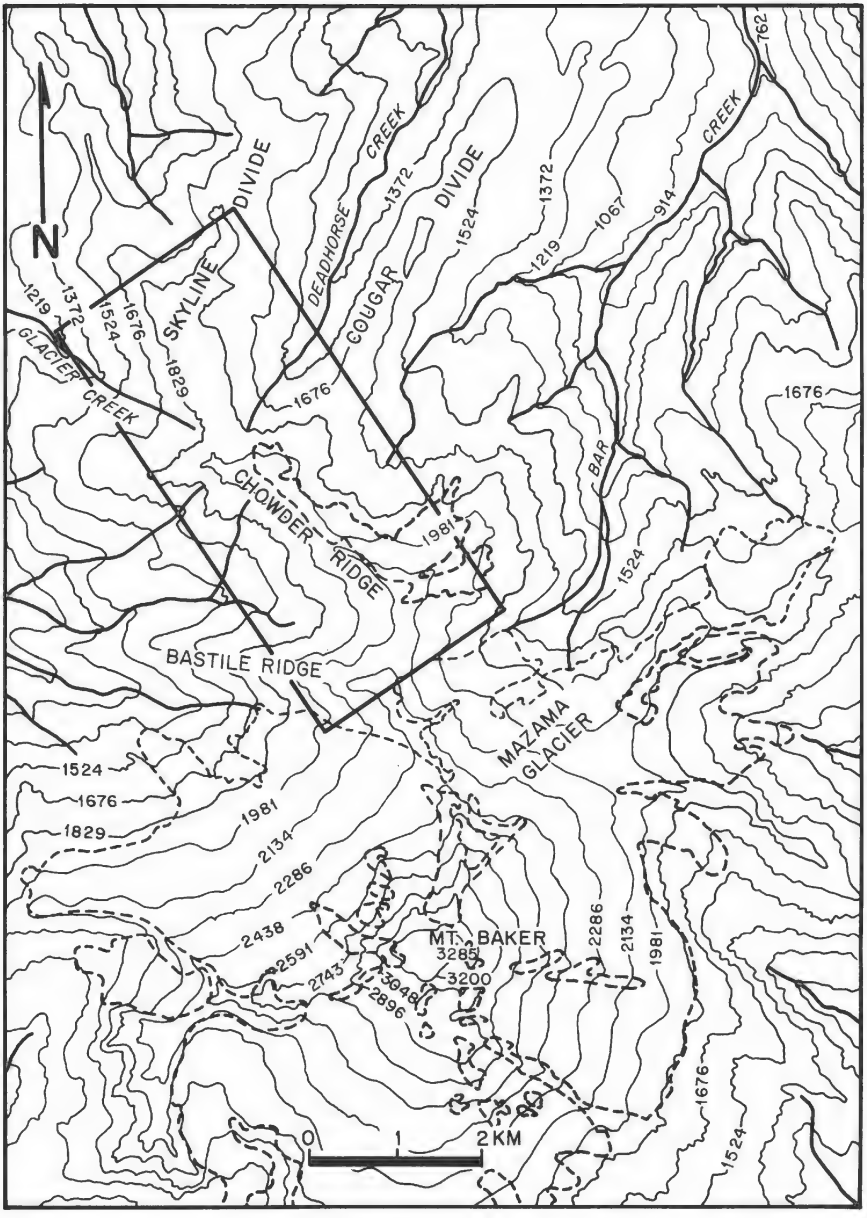

Figure 1. Map of Chowder Ridge and surrounding area. Elevation is given in meters with topographic lines separated by approximately 152 m (500 ft). The area enclosed within the rectangle is proposed as an alpine research natural area.

of the Nooksack Group. This group is of late Jurassic and early Cretaceous age and consists of graywackes, siltstones, granite rocks, and limestone boulders. The group is fossiliferous and appears to have been formed during a period of rapid marine accumulation. The marine fossils are responsible for the name "Chowder Ridge." Uplift and deformation of the sedimentary rocks is shown by folded, sometimes nearly vertical beds. The ridge itself appears to be an arete formed by Pleistocene alpine glaciers. Glacial remnants are seen along the northeast slope, especially in the area where Chowder joins Bastile Ridge. Here the Chowder Glacier abuts against the northwest lobe of Mazama Glacier (see Fig. 1).

Weathering and erosion have been dominant factors in shaping Chowder Ridge and in establishing superficial landforms. Extensive deposits of pebbles and boulder-size sediments funnel into the three principal streams containing runoff water from the ridge. These streams, Bar Creek, Deadhorse Creek, and Glacier Creek, eventually empty into the north fork of the Nooksack River.

The sedimentary origin of Chowder Ridge is an unusual and interesting feature. Other mountain formations immediately associated with Chowder Ridge are apparently composed primarily of andesite. These include Skyline Divide, Cougar Divide, Bastile Ridge, and Mt. Baker itself.

Predominant Animal-Life

The most conspicuous animals of Chowder Ridge are mountain goats which graze the south slopes during the summer but apparently spend the winter on better protected ridges such as Barometer Mountain in the Wells Creek area. The most common inhabitants, however, are rodents, several species of which are known to occur on Chowder Ridge or may be expected to live there given their distribution on adjacent Cougar and Skyline Divides. The largest and most obvious of these is the hoary marmot *(Marmota caligata)* which frequents both the northern and southern slopes of Chowder Ridge, building its den near or below snowfields. Here water-release continues through the summer, providing an abundance of vegetation for the herbivorous marmot. Pikas *(Ochotona princeps)* are common on Cougar Ridge and may be expected in suitable rock formations on Chowder. Unlike the marmot which hibernates, the pika remains active through the winter, feeding on "hay piles" stored during summer. One of the most common rodents of mountain meadows in the Mt. Baker area is the heather vole *(Phenacomys intermedius)*. As the name suggests, this mouse is normally found in heather meadows where it remains active through the winter, building nests of grasses and sedges beneath the snow and heather. It excavates rather extensive tunnel and room systems under the snow and feeds on nearby vegetation. As the snow melts, the nests and latrine piles are readily seen scattered over the meadows. The water rat *(Microtus richardsonii)* also builds nests and tunnel systems under the snow, but usually not in heather communities. The tunnels are often earth-filled and as the snow melts they appear as shallow elongate mounds, often several meters long, or rutted runways through the vegetation. Two other mice of the area are the forest deer mouse *(Peromyscus oreas)* and the Pacific jumping mouse *(Zapus trinotatus)*, the latter hibernating during the winter. Mice are most prevalent in the subalpine zone, on the north slope of Chowder near Cougar Divide. The upper south slopes are used most extensively in early summer. As the alpine meadows become dry in the summer, the mice migrate

downward, returning in early fall. Chipmunks *(Eutamias townsendi)* are common inhabitants of subalpine areas, especially among tree clumps. Occasionally they also range upward into the alpine zone.

Carnivores of Chowder include such transient hunters as the cougar and coyote. The wolverine has also been reported to be in the area (Senger, pers. com.). The insectivorous dusky shrew *(Sorex obscurus)* is a frequent inhabitant of the area and is active all winter. Finally, deer and bear may be expected in the subalpine areas of both the north and south slopes.

Although no attempt has been made to inventory the birds of Chowder Ridge, two species deserve mention. These are blue grouse *(Dendrogapus obscurus)* of subalpine habitats, and ptarmigan *(Lagopus leucurus),* a common inhabitant of the rugged alpine slopes.

Vegetation: Method of Analysis

The quantitative data presented in this paper are part of a more extensive study involving alpine plant communities of the North Cascades Range (Douglas, 1973; Douglas and Bliss, 1977). In that study fifteen stands were quantitatively sampled in the alpine zone of Chowder Ridge and subalpine stands were qualitatively described. Determinations of vegetative patterns have been based on these analyses plus additional observations by the authors.

The term "stand" refers to a particular example of homogeneous vegetation which was sampled. "Community" or "community type" is a grouping of similar stands. Each stand was quantitatively sampled with twenty 20 x 50 cm quadrats set out (perpendicular to the slope contours) by a restricted random technique (Bliss, 1963) in a 5 x 10 m area. Crown cover, using the methods and cover classes of Daubenmire (1959, 1968), was estimated for all vascular plant species in each quadrat. Frequency and average cover for each species were calculated and converted to prominence values by multiplying the average percentage cover by the square root of the species frequency in each stand, a modification of the procedure used by Beals (1960). This index provides a technique by which cover and frequency may be combined into a single value for use in mathematical equations and in constructing shorter and more easily interpreted tables (see Fig. 2).

Similarity coefficients (C) between stands were then computed using the formula $C = 2w/(a+b) \times 100$ (Gleason, 1920). In this formula, w is the sum of the lowest prominence values of species common to both stands, and a and b are the total prominence values of all species in stands a and b. Species were not adjusted in relation to their maximum values of frequency and cover. Dissimilarity values $(1-C)$ were then computed and used for the construction of two-dimensional ordinations following Bray and Curtis (1957) and Beals (1960). The ordinations allowed the groupings of stands into community types that are correlated with several environmental gradients.

Results and Discussion

Zonal Patterns—The vegetative zones on Chowder Ridge were shown to be distinct and readily recognizable. The montane zone or closed forest ends abruptly at approximately 1,500 m and is more or less restricted by the topography to the western end of the ridge. Because of prominent snowfields and glaciers on the northern slopes, the

subalpine zone[1] is restricted to the south side and western end of the ridge. Even here, the subalpine vegetation is limited to a narrow band, probably because of the steep (approximately 45 percent) slope and prevailing aspect, resulting in less snow accumulation, earlier snowmelt, and more rapid runoff. The resulting xeric conditions are more favorable to alpine vegetation. Because of these factors, the alpine zone is very extensive and comprises the greater part of the vegetation on Chowder Ridge.

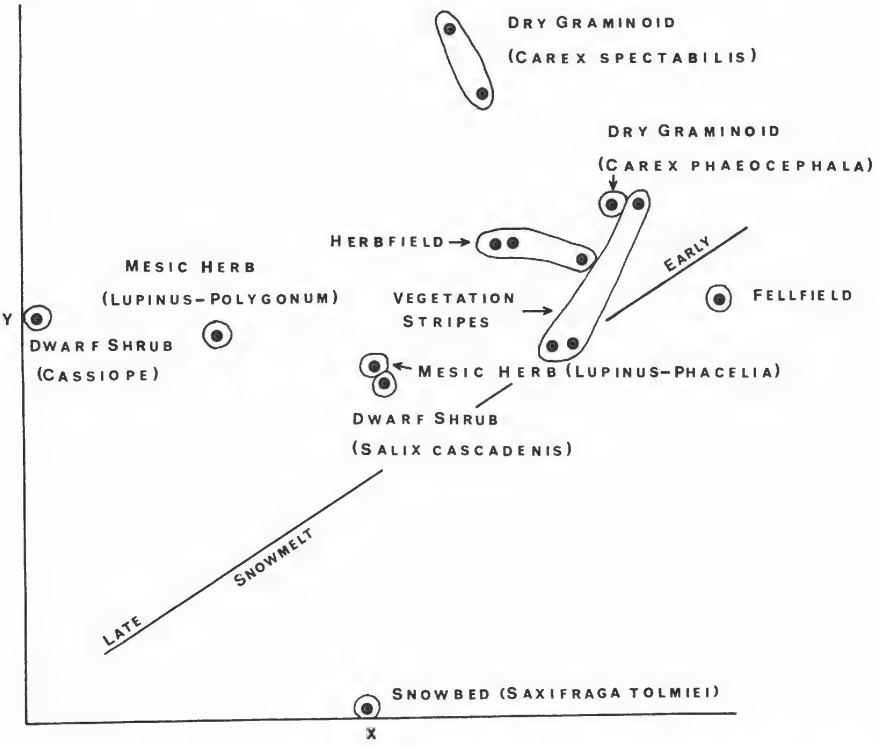

Figure 2. Ordination of 15 stands sampled in the alpine zone on Chowder Ridge, Mt. Baker. Lines delimit community types whose names, where appropriate, are derived from the dominant species.

Community Patterns—The major plant communities in the subalpine and alpine zones of Chowder Ridge are usually sharply delineated and create a complex mosaic over the landscape. This patterning of communities is a response to various environmental parameters, especially wind amount (and its influence on evapotranspiration), snow depth, and time of snowmelt. According to Bliss (1969, 1971), these factors are the most important in determining plant community structure at high elevations throughout western North America.

[1] The subalpine zone is defined here as that area above the montane (closed) forest and below the upper limit of conifers as an upright tree form. Above this is the alpine zone where tree species occur only in a dwarfed or krummholz form (Douglas, 1972, 1973, 1974; Douglas and Bliss, 1977).

Plant Community Types—Eight community types were recognized in the subalpine and alpine zones of Chowder Ridge. Six of these represent habitat-physiognomic types whereas the other two (fell-fields and vegetation stripes) are associated with patterned ground. The vegetational composition and structure and the topographic characteristics of these community types are described below.

Subalpine Zone

Mesic Herb Communities—These communities are dominated by herbs 10 to 40 cm tall and occur on moist, fairly well to well-drained sites. On steep slopes where snowmelt is earlier, *Carex spectabilis* forms a lush, dominant cover. Important associates are *Lupinus latifolius* var. *subalpinus* and *Polygonum bistortoides*. On more moderate slopes where snow accumulation is greater, *Luetkea pectinata* is the dominant species. A number of other species are also of importance on these latter sites. Some of these species are *Deschampsia atropurpurea* var. *latifolia, Carex spectabilis, Castilleja parviflora* var. *albida,* and *Hieracium gracile* var. *gracile.*

Dwarf Shrub Communities—This community type is characterized by low (10 to 30 cm) ericads and occurs on the more mesic slopes or sporadically along the lower flanks of the ridge. These communities may be dominated by either *Cassiope mertensiana* and *Phyllodoce empetriformis* or *Vaccinium deliciosum.* In stands where *Cassiope* and *Phyllodoce* dominate, *Vaccinium deliciosum* and *Luetkea pectinata* are conspicuous components. Where *Vaccinium deliciosum* is the major species, *Phyllodoce empetriformis* and *Luetkea pectinata* are also important elements. The ecological differences associated with this change in floristic composition is not well known, although the *Vaccinium* dominated stands are more often, but not exclusively, found in close proximity to subalpine tree clumps (Douglas, 1972).

Snowbed Communities—In depressions or on gentle slopes where snow accumulates and persists until mid- or late summer, *Carex nigricans* forms a continuous mat of vegetation. Frequent associates of *C. nigricans* in these snowbed communities are *Epilobium alpinum* var. *alpinum* and *Luetkea pectinata,* both with low cover values.

Tree Clump Communities—On Chowder Ridge, tree clumps, although conspicuous, are restricted to a relatively limited band along the southwest to west flanks of the ridge. These stands are found on mesic mounds or ridges which are the first areas to become snow free in the subalpine zone. They are dominated mainly by *Tsuga mertensiana* and *Abies amabilis* with occasional occurrences of *Abies lasiocarpa* and *Chamaecyparis nootkatensis.* The understory of these tree clumps is variable depending on density. In open stands, *Vaccinium membranaceum, A. amabilis, T. mertensiana,* and *Phyllodoce empetriformis* are common while in closed stands understory vegetation is sparse. On the periphery of most clumps a band of tall shrubs (e.g., *V. membranaceum, Rhododendron albiflorum, Sorbus sitchensis* var. *grayi*) is generally present. This peripheral vegetation is probably a response to the more favorable microenvironment provided by the tree clump (Douglas, 1972).

Alpine Area

Since quantitative data are available for most of the alpine community types, an ordination illustrating the floristic relationships of the stands has been constructed (Fig. 2). The stand groupings or community types are correlated with particular environmental

factors, the most obvious of which are time of snowmelt and subsequent moisture availability.

Mesic Herb Communities—At lower elevations in the alpine zone, where snow persists slightly longer, the steep slopes are dominated by a lush herbaceous cover. These sites remain moist throughout much of the growing season due to melting of snowbanks upslope. *Lupinus latifolius* var. *subalpinus* is the most prominent species in these stands (Table 1). Other important plants are *Polygonum bistortoides, Vaccinium*

TABLE 1. Composition of alpine plant community types on Chowder Ridge, Mt. Baker. Data are for prominence value indices.[a]

	Community Types									
Species	S-ST[b] (1)[c]	DS-CM (1)	DS-SC (1)	MH-LP (1)	MH-LPh (1)	DG-CP (1)	DG-CS (2)	HF (3)	VS (3)	FF (1)
Saxifraga tolmiei	226									
Juncus drummondii var. subtriflorus	27									
Luzula piperi	26		16	37						
Carex nigricans	14	8		6						
Carex spectabilis	2	44	20	105		5	533			
Cassiope mertensiana		369								
Vaccinium deliciosum		320		249						
Phyllodoce glanduliflora		296								
Luetkea pectinata		286		136						
Sibbaldia procumbens		5				14	80			
Hieracium gracile		5		40						
Polygonum bistortoides		4		389						
Deschampsia atropurpurea		4		79						
Potentilla flabellifolia		T								
Salix cascadensis			324							
Festuca ovina var. brevifolia			8			41	40		14	10
Luzula spicata			3			18	6	4	4	
Penstemon procerus var. tolmiei			2	3			2		T	
Antennaria umbrinella			1				17	1		
Lupinus latifolius var. subalpinus				865	598					
Trisetum spicatum				14			T	16	3	T
Erigeron peregrinus var. scaposus				12						
Poa cusickii var. purpurescens				10						
Arnica latifolia var. gracilis				8						
Phlox diffusa var. longistyla				6		160	155	250	36	85
Carex rossii				6						
Phacelia heterophylla var. pseudohispida					57					
Epilobium alpinum var. lactiflorum					2					
Poa cusickii var. epilis					2					
Carex phaeocephala						236	3	49	5	34
Solidago multiradiata var. scopulorum						96	125	141	37	33
Oxytropis campestris var. gracilis						94		147	36	50
Carex breweri var. paddoensis						36	134			
Selaginella densa						36	2	48	7	51

TABLE 1. (Continued)

Potentilla diversifolia	31	4	232	8	4
Haplopappus lyalli	18		2		
Campanula rotundifolia	2	2	1	1	4
Cerastium arvense	1	1	52	25	2
Sedum lanceolatum	1	2	13	2	
Antennaria alpina var. media		42		9	
Lupinus lepidus var. lobbii		10		2	
Achillea millefolium ssp. lanulosa var. alpicola		1	74	9	
Veronica cusickii	1				
Agrostis scabra		T			6
Carex albonigra			97	8	
Poa alpina			62	7	
Antennaria rosea			17		
Draba praealta			8	T	
Silene acaulis var. escapa			4	15	
Draba lonchocarpa			1	T	
Potentilla fruticosa			1	2	
Phacelia sericea			1	7	1
Saxifraga occidentalis			1		
Draba incerta			1	2	
Silene parryi			T		
Agropyron caninum var. latiglume				10	
Castilleja rupicola				4	
Erigeron compositus var. glabratus				3	
Potentilla villosa var. parvifolia				1	18
Taraxacum ceratophorum				1	
Arenaria rubella				T	
Stellaria longipes var. altocaulis				T	
Saxifraga bronchialis var. austromontana					3

[a] T (trace) indicates a prominence value of less than 0.5.

[b] Abbreviations for community types and dominant species: S-ST = Snowbed—*Saxifraga tolmiei;* DS-CM = Dwarf shrub—*Cassiope mertensiana;* DS-SC = Dwarf shrub—*Salix cascadensis;* MH-LP = Mesic herb—*Lupinus latifolius—Polygonum bistortoides;* MH-LPh = Mesic herb—*Lupinus latifolius—Phacelia heterophylla;* DG-CP = Dry graminoid—*Carex phaeocephala;* DG-CS = Dry graminoid—*Carex spectabilis;* HF = Herbfield; VS = Vegetation stripes; FF = Fell-field.

[c] Number of stands sampled appears in parentheses.

deliciosum, Luetkea pectinata, and *Carex spectabilis.* The abundance of subalpine elements in these stands indicates their close relationship with subalpine vegetation.

A second alpine mesic herb type occurs locally along the flanks of the ridge between approximately 2,030 and 2,090 m elevation. This band, about 100 m long, occurs on a steep, relatively unstable slope. Species richness is low, with only *Lupinus latifolius* var. *subalpinus* being important (Table 1). Other species present are *Phacelia heterophylla* var. *pseudohispida, Epilobium alpinum* var. *lactiflorum,* and *Poa cusickii* var. *epilis.*

Dry Graminoid Communities—On some of the well-drained, exposed upper slopes and ridgetops, where snow cover melts by early summer, floristically rich communities dominated by sedges are found. The most extensive community of this type is dominated by *Carex spectabilis* (Table 1). These alpine *C. spectabilis* stands are markedly different from those of the subalpine zone. The drier alpine stands are not only richer floristically

but are characterized by prominent alpine elements such as *Phlox diffusa* var. *longistylis, Carex breweri, Sibbaldia procumbens, Solidago multiradiata* var. *scopulorum, Antennaria aplina* var. *media,* and *Festuca ovina* var. *brevifolia.*

The most xeric sites occupied by dry graminoid communities are dominated by *Carex phaeocephala* with important associates including *P. diffusa* var. *longistylis, S. multiradiata* var. *scopulorum,* and *Oxytropis camestris* var. *gracilis* (Table 1).

Dwarf Shrub Communities—Two dwarf shrub communities occur in the alpine zone on Chowder Ridge. The most common is the heath type which has close floristic affinities with the subalpine heath type. In the alpine communities, however, *Phyllodoce empetriformis* is mostly replaced by *P. glanduliflora* and is co-dominant with *Vaccinium deliciosum, Cassiope mertensiana,* and *Luetkea pectinata* (Table 1). Except for the increased elevation and the occurrence of these stands above tree-line, the ecological differences are not readily apparent.

Several small stands dominated by *Salix cascadensis* occur near the crest of the ridge. These nearly pure mats occur in slight depressions (Table 1).

Snowbed Communities—Flat boulder fields are prominent on the eastern end of Chowder Ridge, along the southern flank. Snow accumulates in these sites, resulting in a short growing season. Here vegetative cover is sparse with only *Saxifraga tolmiei* var. *tolmiei* being common in spaces between the boulders (Table 1). Less frequent associates include *Juncus drummondii* var. *subtriflorus* and *Luzula piperi.*

Herb-field Communities—Continuous vegetation comprised of a rich assemblage of plants with a cushion or matted habit occurs on many of the exposed ridgetops. Most of these stands cover a limited area. Some of the more prominent species on these sites are *Phlox diffusa* var. *longistyla, Potentilla diversifolia, Oxytropis campestris* var. *gracilis, Solidago multiradiata, Carex albonigra, Achillea millefolium,* and *Poa alpina* (Table 1).

Fell-field Communities—These sparsely vegetated communities are restricted to relatively level sites along the ridgetop. The plants are scattered, usually in clumps, among the frost-shattered rocks. Characteristic species, with low cover values, are *Phlox diffusa* var. *longistyla, Selaginella densa, Oxytropis campestris* var. *gracilis, Carex phaeocephala, Solidago multiradiata* var. *scopulorum,* and *Saxifraga bronchialis* var. *austromontana* (Table 1).

Vegetation Stripe Communities—Along the south-facing flank of the ridge, on the upper slopes near the ridge tops, the vegetation is arranged in long stripes 20 to 40 cm wide, each separated by about 1 m of scree material. This striping is a result of the downslope creep of the unstable substrate. Floristically, the composition of these communities is similar to that found in the fell-fields (Table 1). Some of the more common species in the vegetation stripes are *Solidago multiradiata* var. *scopulorum, Phlox diffusa* var. *longistyla, Oxytropis campestris* var. *gracilis, Cerastium arvense, Silene acaulis* var. *escapa,* and *Festuca ovina* var. *brevifolia.*

Krummholz Communities—In the lower part of the alpine zone, along the southern flanks of the ridge, clumps of dwarfed tree species (krummholz) occur. Because of their ability to accumulate snow, these stands become snow free later than all other communities except those of snowbeds. *Abies lasiocarpa* is the dominant species with *Tsuga mertensiana* occurring infrequently. Understory vegetation is usually sparse or lacking.

Floristics

Several factors have contributed to the interesting nature of the floristics of the Chowder Ridge area. The area has contrasting habitats, especially those associated with steep, dry, southerly slopes and those of cool, snowy, equally steep north slopes. The climatic conditions of the south slopes resemble those of the eastern Cascades and northern Rockies, resulting in an unusual mixture of relatively drought-tolerant species. Finally, the Chowder Ridge area is located at the southern limit of glaciation, with consequential representation of northern and southern species. These and other features contribute to the floristic diversity and species richness of the area.

The species of the area can for convenience be divided into three major categories: (1) typical representatives of the western North Cascades; (2) species typically occurring in the eastern Cascades and northern Rockies; (3) plants representing range extensions of more northerly distributed species. These categories, especially the latter two, are not clearly distinct. The first group is naturally the largest and includes most of the dominants of the area, which as such are discussed in the plant communities section of this paper. The second group includes several species, the most notable of which are briefly discussed below. The general range of such species is cited from Hitchcock *et al.* (1955-1969).

Arnica rydbergii—This is an uncommon plant on Chowder Ridge and has rarely been collected at other locations in the North Cascades (Taylor *et al.,* 1973). It is generally found in the northern Rockies and eastern Cascades, extending south into California.

Astragalus alpinus—This is a circumpolar species which is common in the alpine zone of the Rocky Mountains. It is well known from the eastern Cascades but has rarely been collected west of the Cascade crest. It is an occasional plant on Chowder Ridge.

Carex breweri var. *paddoenis*—This species is fairly common on Chowder Ridge and has frequently been collected by the authors at other locations in the western North Cascades (Taylor *et al.,* 1973). Previously it was thought to be restricted to the eastern Cascades and Rocky Mountains.

Carex capitata—This is a circumboreal species which is common throughout much of the Rocky Mountains, extending west to the Sierra Nevadas of California. Prior to collections by the authors (Taylor *et al.,* 1973), this sedge was not known from Washington, and Chowder Ridge is the only location where it is known to occur west of the Cascade crest.

Carex nardina—This is another circumboreal sedge which is widespread in the Rocky Mountains. Collections by the authors indicate a rather broad range for this species in the North Cascades, including Chowder Ridge (Taylor *et al.,* 1973).

Draba ventosa var. *ruaxes*—*Draba ventosa* is chiefly a Rocky Mountain taxon and the var. *ruaxes* is known only from a few collections from the Glacier Peak area (Taylor *et al.,* 1973) and Chowder Ridge.

Eriogonum umbellatum—This desert buckwheat is extremely common in the Rocky Mountain area and Great Basin plains. It occasionally occurs in the eastern Cascades but seldom on the west side (especially in the North Cascades). Both *E. umbellatum* var. *subalpinum* and var. *hausknechtii* occur in the Chowder Ridge area.

Poa rupicola—This bluegrass is common throughout much of the Rocky Mountains but was not known to occur in the Cascades until 1970 (Douglas and Taylor, 1970).

It has now been collected at two locations in the North Cascades, Chowder Ridge and Hoodoo Pass, Chelan County (Taylor *et al.,* 1973).

Salix nivalis—This dwarf apline willow is known to occur at several locations in the North Cascades, including the Chowder Ridge area. However, it is much more prevalent in the high mountains of the Rockies.

Vaccinium occidentale—This species of huckleberry or blueberry is fairly common in the northern Rocky Mountains and is well known on the east side of the Cascades; however, it has rarely been collected west of the Cascade crest. In the Chowder Ridge area (SE end of Skyline Divide) it is a local dominant on a windswept plateau (Taylor *et al.,* 1973).

Vaccinium scoparium—Grouseberry is a very common species in the understory of coniferous forests in the eastern Cascades and especially in the Rocky Mountains where it occasionally extends upward into the alpine zone. The Chowder Ridge area is the only location where this species is known to occur west of the Cascade crest.

The third floristic group is smaller and cannot easily be distinguished from the previous group in that representative species may occur in the northern Rockies. However, species of the third group are generally associated with tundra environments of northern Canada and Alaska. This group constitutes an interesting part of the Chowder Ridge area flora. The most notable species are listed and briefly discussed below.

Aster sibiricus—This is a circumboreal species, extending southward in the northern Rockies as well as in the Cascades. However, the southern limit of its distribution in the Cascade Range appears to be the Mount Baker area. It is fairly common on Chowder Ridge.

Empetrum nigrum—This species is by no means restricted in the Cascades to the Chowder Ridge area, but it is an important cushion plant there. It achieves its best development in the arctic-alpine tundra of northern Canada and Alaska.

Gentiana glauca—This small gentian is common in the tundra of northern Canada and Alaska. In Washington, it has now been collected at two locations, the Chowder Ridge area (SE Skyline Divide) and Horseshoe Mt. in Okanogan County (Douglas and Taylor, 1970; Taylor *et al.,* 1973).

Lycopodium alpinum—This is an attractive and distinctive circumboreal clubmoss which has extended southward along mountain ranges. In the Cascades it reaches Washington where it is known to occur at only a few sites, one the Chowder Ridge area (Taylor *et al.,* 1973).

Saxifraga oppositifolia—This is a rare alpine plant in the North Cascades, being known from only a few locations including Chowder Ridge. It is well known, however, in more northern environments, the northern Rockies, and northeastern North America.

A few species occurring in the Chowder Ridge area are at or near the northern limit of their distribution; for example, *Arnica nevadensis,* primarily of the Sierras. Other unusual plants are rare color variants of common alpine species. These include white-flowered forms of both *Lupinus lepidus* var. *lobbii,* and *Silene acaulis.* The yellow-flowered variant of *Claytonia lanceolata* (previously *C. lanceolata* var. *chrysantha,* see Douglas and Taylor, 1972) occurs in a local population at the SE end of Skyline Divide. Finally, a number of relatively uncommon, typically Cascade plants are scattered over the Chowder Ridge area.

Although the moss flora of Chowder Ridge has not been systematically studied,

there is little doubt that a careful inventory would yield "unusual" species. For example, *Pohlia erecta,* previously known in western North America from only two collections, one from Mount Rainier and the other from the British Columbia Cascades (W. B. Schofield, pers. comm.), has been collected[2] in a fell-field community along the ridge crest.

Plant collections taken by the authors from the Chowder Ridge area (including Chowder Ridge and the northwest-southeast segment of Skyline Divide) are alphabetically listed in Table 2.

TABLE 2. Plant collections from the Chowder Ridge area.[a]

Achillea millefolium lanulosa alpicola—D 2239, T 1270
Agoseris aurantiaca aurantiaca—D 2253, DD 4375
Agropyron caninum majus latiglume—D 2241, D 2278, T 1274, T 2589
Agrostis idahoensis—T 2184
A. scabra—T 1277, T 2610
Androsace septentrionalis subumbellata—D 2305, T 4322
Anemone drummondii—T 1662
A. multifida hirsuta—T 2609
A. multifida multifida—D 2276, T 728
Antennaria alpina media—D 2244, D 2407, DD 4289, DD 4312, T 3122, T 3145
A. microphylla—D 2306, D 4255, DD 4370, T 3524
A. umbrinella—D 4305a, DD 4356
Arabis lyallii—D 2330, T 1643, T 1647
Arenaria nuttallii—T 1659
A. obtusiloba—D 2331
A. rubella—T 3534
Arnica latifolia gracilis—DD 4373
A. nevadensis—T 3531
A. rydbergii—T 3532
Aster foliaceous foliaceous—DD 4374
A. sibiricus meritus—D 2251, DD 4346, T 743
Astragalus alpinus—T 1663
Campanula rotundifolia—D 2242, T 751
Cardamine oligosperma kamtschatica—D 4271 (specimen not retained)
Carex albonigra—D 2237, DD 4349, T 1909
C. breweri paddoensis—T 3526
Carex capitata—DD 4285, DD 4345
C. nardina—DD 4335
C. nigricans—D 2270, T 1280, T 2602
C. phaeocephala—D 2245, D 2289, DD 4355, T 1281, T 1284, T 2587
C. pyrenaica—D 2262, T 1281
C. rossii—D 2265
C. spectabilis—D 2271, D 2408, T 1283, T 2601
Cassiope mertensiana—T 3142, T 5213
Castilleja parviflora albida—D 2290, T 736
C. rupicola—D 2277, DD 4288, T 1656, T 2608
Cerastium arvense—D 2240, T 744
Claytonia lanceolata—D 2141 (yellow form), D 2142, T 3149, T 3151 (yellow form)
Deschampsia atropurpurea—D 2266, T 764, T 1923
Draba incerta—DD 4264, T 4321
D. lonchocarpa—DD 4250b, DD 4254b, DD 4267b, DD 4272, T 1282, T 1657, T 1658, T 3529
D. paysonii trealeasii—DD 4347, T 1650, T 3144
D. praealta—D 2284, DD 4250a, DD 4254a, DD 4267a, DD 4350, T 1649, T 2583
D. stenoloba—DD 4248, T 3123
D. ventosa ruaxes—D 2280
Empetrum nigrum—T 3125
Epilobium alpinum clavatum—DD 4371
E. alpinum lactiflorum—DD 2257, T 1654
E. latiflolium—T 729
Eriogonum umbellatum subalpinum—D 2295
E. umbellatum hausknechtii—T 2182

[2] Collection was made by Tony Basabe, graduate student, Western Washington University.

TABLE 2. (Continued)

Erigeron compositus glabratus—D 2250, DD 4348, T 732, T 1266
E. peregrinus callianthemus scaposus—D 2287, DD 4274
E. peregrinus peregrinus peregrinus—DD 4376
Festuca ovina brevifolia—D 2248, T 765, T 1272
Gentiana glauca—D 2348, DD 4306, T 1232
Haplopappus lyallii—D 2243, T 741, T 1267, T 2592
Hieracium gracile—D 2297, T 3133
Juncus drummondii subtriflorus—D 2260, T 2599
J. parryi—D 2293, T 772
Lomatium martendalii—D 2300, T 748
Luetkea pectinata—D 2292, T 3127
Lupinus latifolius subalpinus—D 2256, T 3141
L. lepidus lobbii—D 2272, T 1223, T 2603
Luzula piperi—D 2261, D 2269, T 1235
L. spicata—DD 4278, T 3533
Lycopodium alpinum—D 2337
Mimulus tilingii caespitosa—T 2591
Oxytropis campestris gracillis—T 734, T 3137
Oxyria digyna—T 2605
Penstemon davidsonii menziesii—T 708, T 730, T 1221
P. procerus tolmiei—D 2263, D 2288, T 1217
Phacelia heterophylla pseudohispida—D 2258
P. sericea sericea—T 1269, T 1647
Phleum alpinum—T 758, T 1278
Phlox diffusa longistylis—T 755
Phyllodoce empetriformis—T 3143
Phyllodoce glanduliflora—T 1229
Poa alpina—D 2247, DD 4251, DD 4269, T 1276, T 2580, T 2597
P. cusickii epilis—D 2255, D 2304, DD 4377, T 762, T 763, T 2588
P. cusickii purpurescens—D 2267
P. gracillima—T 1273, T 1275, T 1279, T 1906, T 2581
P. incurva—T 2611
P. lepticoma paucispicula—T 1653, T 2598
P. rupicola—DD 4152, T 762, T 763, T 1968
P. sandbergii—D 2252, D 2281, DD 4353, T 1644
Polygonum bistortoides—T 3130
P. viviparum—D 2334, T 737, T 1665
Potentilla diversifolia diversifolia—D 2279, DD 4258, DD 4273, T 1228, T 3132
P. flabellifolia—D 2264, T 1177, T 1230
P. fruticosa—D 2254, T 740
P. villosa parvifolia—D 2282, DD 4311, T 1655
Polemonium elegans—T 1646
Ranunculus eschscholtzii eschscholtzii—DD 4369
Salix cascadensis—D 2329, D 2332, D 2333, D 2335, D 2338, T 1660, T 1661, T 3487, T 3488, T 3489
S. nivalis saximontana—D 2336, DD 4308, T 3490
Saxifraga bronchialis austromontana—D 2299, T 746
S. caespitosa emarginata—T 3528
S. debilis—DD 4365, DD 4366
S. ferruginea macounii, T 749
S. lyallii—DD 4367
Saxifraga occidentalis occidentalis—D 2301, DD 4263, T 3527
S. odontoloma—DD 4344
S. oppositifolia—DD 4247
S. punctata cascadensis—DD 4368, T 1664
S. tolmiei tolmiei—D 2259, T 739, T 1234
Sedum divergens—D 2302, T 3128
S. lanceolatum lanceolatum—D 2249, D 2286, T 747, T 1645
S. roseum integrifolium—D 2273, T 1651
Selaginella densa—T 2183
Senecio elmeri—DD 4225, T 1271
Sibbaldia procumbens—D 2303, T 1636
Silene acaulis escapa—D 2285, T 733, T 1224, T 1263
S. parryi—D 2291, D 2298, DD 4354, T 745, T 3131
Sitanion hystrix hystrix—D 2283, T 2185
Smelowskia ovalis—T 1652
Solidago multiradiata scopulorum—D 2238, T 3140
Stellaria longipes altocaulis—DD 4280, T 3530

TABLE 2. (Continued)

Taraxacum ceratophorum—D 2253, DD 4226, T 2586
Trisetum spicatum—D 2246, D 2268, T 757
Vaccinium caespitosum—DD 4246
V. deliciosum—T 1239, T 1637
V. occidentale—DD 4361
V. scoparium—D 2349
Veronica cusickii—D 2406, T 742, T 1220

[a] Chowder Ridge area includes Chowder Ridge and the adjacent northwest-southeast section of Skyline Divide.

Specimens are maintained in the herbaria of Western Washington University, Bellingham, Washington; University of Alberta, Edmonton, Alberta; or G. W. and G. G. Douglas, Victoria, British Columbia. Specimens are cited by collector (D = Douglas, DD = Douglas & Douglas, T = Taylor) and collector number. Nomenclature follows Hitchcock and Cronquist (1973).

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Literature Cited

Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72: 156-181.
Bliss, L. C. 1963. Alpine plant communities of the Presidential Range, New Hampshire. Ecology 44: 678-697.
———. 1969. Alpine community patterns in relation to environmental parameters, pp. 167-184. *In* K. N. H. Greenridge (ed.), Essays in Plant Geography and Ecology. Nova Scotia Museum, Halifax, Nova Scotia.
———. 1971. Arctic and alpine plant cycles. Ann. Rev. Ecol. and Syst. 2: 405-438.
Bray, J. R., and J. T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325-349.
Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northw. Sci. 33: 43-66.
———. 1968. Plant Communities. Harper and Row, New York. 300 pp.
Douglas, G. W. 1971. The alpine-subalpine flora of the North Cascade Range, Washington. Wasman J. Biol. 29: 129-168.
———. 1972. Subalpine plant communities of the western North Cascades, Washington. Arct. Alp. Res. 4: 147-166.
———. 1973. Alpine Plant Communities of the North Cascades Range, Washington and British Columbia. Univ. of Alberta, Edmonton. Ph.D. Dissertation. 145 pp.
———. 1974. Montane zone vegetation of the Alsek River region, southwestern Yukon. Can. J. Bot. 52: 2505-2532.
———, and L. C. Bliss. 1977. Alpine and high subalpine plant communities of the North Cascades Range, Washington and British Columbia. Ecol. Monogr. 47: 113-150.
———, and R. J. Taylor. 1970. Contributions to the flora of Washington. Rhodora 72: 496-501.
———. 1972. The biosystematics, chemotaxonomy, and ecology of *Claytonia lanceolata* in western Washington. Can. J. Bot. 50: 2177-2187.
Dyrness, C. T., J. F. Franklin, C. Maser, S. A. Cook, J. D. Hall, and G. Faxon. 1975. Research natural area needs in the Pacific northwest—a contribution to land-use planning. USDA For. Ser. Gen. Tech. Rep. PNW-38. 231 pp.
Easterbrook, D. J., and D. A. Rahm. 1970. Landforms of Washington. Union Printing Co., Bellingham, WA. 156 pp.
Federal Committee on Research National Areas. 1968. A Directory of Research Natural Areas on

Federal Lands of the United States of America. Washington, D.C., Superintendent of Documents, 129 pp.
Franklin, J. F., and J. M. Trappe. 1963. Plant communities of the North Cascades Range: a reconnaissance. Northw. Sci. 37: 163-164 (abstract).
————, and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. U.S.F.S. Res. Paper PNW-80. 216 pp.
Gleason, H. 1920. Some applications of the quadrat method. Bull. Torr. Bot. Club 47: 21-33.
Gorman, M. W. 1907. Vegetation of the northeast slope of Mt. Baker. Mazama 3: 31-48.
Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Wash. Press, Seattle. 730 pp.
————, ————, M. Ownbey, and J. W. Thompson. 1955-1969. Vascular Plants of the Pacific Northwest, Vols. 1-5. Univ. Wash. Press, Seattle.
Misch, J. 1966. Tectonic Evolution of the Northern Cascades of Washington State. Inst. Mining and Metallurgy Spec. Vol. 8: 101-148.
Muenscher, W. C. 1941. The Flora of Whatcom County, State of Washington. Author, Ithaca, N.Y. 134 pp.
Romancier, R. M. 1974. Natural area programs. J. For. 72: 37-42.
St. John, H., and E. Hardin. 1929. Flora of Mt. Baker. Mazama 11: 52-102.
Taylor, R. J., G. W. Douglas, and L. M. Sundquist. 1973. Contributions to the flora of Washington. II. Northw. Sci. 47: 169-179.

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Freshwater Triclads (Turbellaria) of Washington

Abstract

During a survey of freshwater habitats in Washington state, three genera of triclad flatworms *(Polycelis, Dugesia,* and *Phagocata)* were observed in such diverse environments as springs, streams, lakes, caves, and temporary ponds. Field data which included the temperature, pH and elevation of collection sites indicated that 1) *Polycelis* was restricted to relatively cold habitats such as springs and small montane streams; 2) *Dugesia* was common in lowland lakes and larger streams with more variable temperatures; and 3) *Phagocata* was found at a single locality, a temporary pond which was present for only three months of the year. The relationship between these ecological differences and the different life history strategies exhibited by these genera is discussed.

Introduction

Systematic statewide studies of freshwater flatworms in North America have added much to the understanding of this rather widespread and ecologically diverse group of aquatic organisms. In particular the work in Virginia (Kenk, 1935), Michigan (Kenk, 1944), Alaska (Kenk, 1953), Tennessee (Darlington and Chandler, 1972), and New Mexico (Chandler and Darlington, 1975) has increased our knowledge of the distribution and natural history of triclads greatly. No such systematic study has been undertaken in any of the states of the Pacific Northwest, and this report is an attempt to provide information of this nature from Washington and present comparative data from a wide range of freshwater habitats.

Methods and Materials

This survey was conducted throughout Washington state during 1973 and 1974, and as many types of freshwater environments as possible were examined. Thirty-three collection sites from fourteen Washington counties were included in the study, and the temperature and pH of the habitats were recorded at most sites. Flatworm collections were carried out for 30 minutes at each site and the number of individuals collected can be used to approximate relative population sizes. When utilizing these measures of relative frequency in comparisons between populations of different species, considerable error may be introduced because of differences in substrate preference. However, this type of behavioral variation is probably minimal within species except in cases of extreme environmental dichotomy such as between cave and epigean streams (see Nixon, 1974).

Following species identification of the collected specimens, microscopic observations were made in order to ascertain the frequency of sexual maturity in the populations. The term "mature" for each species listed below includes all individuals possessing reproductive organs, regardless of the degree of development. Use of this term should not imply that all individuals in this category were involved in sexual reproduction nor

that sexual reproduction occurs necessarily in populations containing mature individuals, for as Kenk (1973a) has pointed out in the case of *Polycelis,* although sexually mature individuals have been observed from many localities at different seasons, no egg capsules or cocoons have ever been observed in the North American species.

Results

Polycelis coronata (Girard)

This species was first described fully by Hyman (1931) from South Dakota, and subsequently has been reported from Colorado (Kenk, 1952), Alaska (Kenk, 1953; Holmquist, 1967), Utah (Beck, 1954; Braithwaite, 1962; Carpenter, 1969), Oregon (Hyman, 1963; Kenk, 1973a), Alberta (Ball and Fernando, 1968), New Mexico (Kenk, 1973a; Chandler and Darlington, 1975), and Montana, Wyoming, and Idaho (Kenk, 1973a). In 1937, D. M. Pike collected specimens of *Polycelis* from Mt. Rainier National Park, Washington, and Hyman deposited them in the National Museum of Natural History, Smithsonian Institution, under the name *P. coronata* (Kenk, 1973a).

Throughout its range, this species has been shown to be restricted to springs and streams of relatively low temperatures, and this finding was also characteristic of the species in this study. Specimens collected in Washington were observed in habitats ranging from 5 to 14 C which were at elevations of 76 to 1920 meters (250-6300 ft). The localities where pH was measured yielded values between 5.0 and 7.4. Five populations contained sexually mature individuals, and those localities exhibited considerably more narrow ranges in these aspects: temperature 10-11 C, pH 6.5-6.8, elevation 91-488 meters (300-1600 ft). Although mature individuals were collected from June through September, no conclusions can be made involving seasonal variation in this regard because many locations were inaccessible during winter months. The collection sites and field data from each site are listed below.

WHATCOM COUNTY

—spring in Bellingham, 51 individuals collected, 3 mature, 6/11/74, pH 6.5, temperature 11.0C, elevation 91 meters (300 ft).

—small stream near Sehome Hill, Bellingham, 3 collected, none mature, 5/21/74, 12.0C, 76 meters (250 ft).

—small stream on Lake Louise Road near Lake Whatcom, 4 collected, none mature, 5/23/74, 10.0C, 107 meters (350 ft).

—small stream near Lake Whatcom in Bellingham, 2 collected, none mature, 5/14/74, 13.0C, 91 meters (300 ft).

—small stream near Mt. Baker, 24 km (15 miles) east of Glacier, 43 collected, none mature, 9/21/74, pH 6.3, 5.0C, 1402 meters (4600 ft).

—small stream near Glacier Creek on Road 3409, 57 collected, 2 mature, 9/21/74, pH 6.8, 10.0C, 488 meters (1600 ft).

SKAGIT COUNTY

—small stream near Rt. 20, 29 km (18 miles) northeast of Marblemount, 76 collected, none mature, 9/28/74, pH 7.0, 12.0C, 305 meters (1000 ft).

—small stream near Old Cascade Highway, 4.8 km (3 miles) southeast of Marblemount, 62 collected, 2 mature, 9/28/74, pH 6.7, 10.0C, 183 meters (600 ft).

SNOHOMISH COUNTY

—small stream on Mt. Pilchuk, 5 collected, none mature, 8/29/74, pH 6.5, 7.0C, 1463 meters (4800 ft).

—small stream 4.8 km (3 miles) west of Monte Cristo, 211 collected, none mature, 8/29/74, pH 6.8, 9.0C, 732 meters (2400 ft).

—small stream 25.7 km (16 miles) southeast of Darlington, just east of Road 322, 108 collected, 6 mature, 8/29/74, pH 6.8, 10.0C, 427 meters (1400 ft).

—small stream near Big Four Ice Caves, 42 collected, none mature, 8/29/74, pH 6.5, 6.0C, 488 meters (1600 ft).

KING COUNTY

—small stream just east of SR 410, 12.8 km (8 miles) southeast of Enumclaw, 39 collected, none mature, 8/9/74, pH 7.0, 11.0C, 457 meters (1500 ft).

—creek just east of U.S. 2, 8 km (5 miles) west of Stevens Pass, 44 collected, none mature, 8/24/74, pH 6.2, 8.0C, 732 meters (2400 ft).

PIERCE COUNTY

—small stream 4.8 km (3 miles) northeast of Mt. Rainier, 25 collected, none mature, 8/9/74, pH 6.6, 9.0C, 1920 meters (6300 ft).

LEWIS COUNTY

—small stream 17.7 km (11 miles) northeast of Packwood, just east of SR 123, 64 collected, none mature, 8/9/74, pH 7.1, 11.0C, 640 meters (2100 ft).

SKAMANIA COUNTY

—small stream near Pimlico Creek, just north of SR 1302, 71 collected, none mature, 8/10/74, pH 6.4, 9.0C, 823 meters (2700 ft).

—small pool of water near spring in Deadhorse Cave, 21 collected, none mature, 8/10/74, pH 5.0, 6.0C, 884 meters (2900 ft).

—small stream near Swift Creek Resevoir, just south of Mt. St. Helens, 32 collected, none mature, 7/7/74, pH 6.9, 10.0C, 488 meters (1600 ft).

KLICKITAT COUNTY

—small stream just west of Road N84, 4.8 km (3 miles) north of Troutlake, 41 collected, none mature, 8/10/74, pH 6.8, 11.0C, 732 meters (2400 ft).

—small stream just west of Road N88, 3.2 km (2 miles) northwest of Troutlake, 6 collected, none mature, 7/7/74, 8.0C, 579 meters (1900 ft).

YAKIMA COUNTY

—small stream near Bird Creek, just east of Road N80, 14.5 km (9 miles) northeast of Troutlake, 45 collected, none mature, 7/6/74, pH 7.0, 10.0C, 1372 meters (4500 ft).

CHELAN COUNTY

—Bridge Creek, 14.5 km (9 miles) southwest of Leavenworth, 54 collected, none mature, 8/25/74, pH 7.4, 14.0C, 610 meters (2000 ft).

—small stream 16 km (10 miles) southwest of Leavenworth, 3 collected, none mature, 8/25/74, pH 7.1, 9.0 C, 671 meters (2200 ft).

SPOKANE COUNTY

—Big Springs on Mt. Spokane, 48 collected, none mature, 8/24/74, pH 6.5, 6.0C, 1250 meters (4100 ft).

CLALLAM COUNTY

—small stream 25.7 km (16 miles) south of Pt. Angeles, 46 collected, none mature, 8/16/74, pH 6.4, 8.0C, 1554 meters (5100 ft).

JEFFERSON COUNTY

—small stream near Hoh River Visitor Center, 51.5 km (32 miles) southeast of Forks, 86 collected, 4 mature, 8/16/74, pH 6.6, 11.0C, 183 meters (600 ft).

—small stream near Dosewallups Falls, 40.2 km (25 miles) southwest of Quilicene, 53 collected, none mature, 8/17/74, pH 6.8, 9.0C, 457 meters (1500 ft).

Dugesia tigrina (Girard)

This species along with *D. dorotocephala* is the most common and widespread triclad found in North America (Kenk, 1972) and has been reported from many types of freshwater habitats. Hyman (1963) noted the occurrence of both *Dugesia* species in Oregon, but failed to point out if they were found in the same streams and also made no mention of relative abundance. While being common in North America generally (occurring from coast to coast), this species is not nearly as common in Washington, having been found at only four localities. These habitats are considerably warmer than those of *Polycelis* and were all at relatively low elevations. The collection sites of *Dugesia* were:

WHATCOM COUNTY
—Lake Whatcom, 16 collected, none mature, 9/17/74, 17C, 91 meters (300 ft).
—Whatcom Creek (flowing from Lake Whatcom), 23 collected, none mature, 9/17/74, 18C, 91 meters (300 ft).
—Lake Fazon, 48 collected, 6 mature, 9/18/74, 15C, 76 meters (250 ft).

KITSAP COUNTY
—Long Lake, 46 collected, none mature, 8/30/74.

Unlike *Polycelis,* the *Dugesia* populations were observed in habitats with relatively slow water movement. Individuals of *Dugesia* were usually found on the aquatic vegetation in the lakes and were rarely observed on or under stones, whereas in Whatcom Creek most individuals were collected from the undersides of the larger rocks present. This behavior contrasted with that of *Polycelis* individuals which were found exclusively on the undersides of stones, possibly reflecting differences in rates of water flow.

Phagocata sp.

This triclad was found at a single locality in Bellingham, Whatcom County, a temporary pond which was present for only three months of the year. This pond was formed by heavy rainfall and melting snow during April of 1974 and 1975 and became dry by June of each year. Individuals of various sizes (3 to 10 mm) and colors (white, pink, tan) appeared soon after formation of the pond and were very abundant (hundreds of individuals observed) but extremely variable. Reproduction by fragmentation was observed as the pond began to warm and dry, similar to the processes reported in *Phagocata velata* (Stringer, 1909; Castle, 1928; Castle and Hyman, 1934; Kenk, 1944, 1972) and *P. vernalis* (Kenk, 1944, 1972). Further details of this process and illustrations of the Washington forms have been presented elsewhere (Nixon, 1977).

Sphalloplana sp.

A collection of specimens probably belonging to this genus has been made by C. M. Senger in a pool in Deadhorse Cave, Skamania County, during 1975 and 1976 (R. Kenk, pers. comm.). This is the same locality where partially cave-adapted specimens of *Polycelis* have been collected (Nixon, 1975, and this report). Like many cave-adapted forms, the *Sphalloplana* are white, eyeless planarians (Senger, pers. comm.), probably having lost pigmentation through regressive evolutionary processes.

Dendrocoelopsis vaginata Hyman

While not collected by the author in this study, this species has been recorded by Kenk (1973b) from Nigger Creek, Whitman County. Although Kenk does not mention the co-occurrence of this species with other triclads at this locality, B. Z. Lang observed (pers. comm.) that *Dendrocoelopsis, Polycelis, Phagocata* and *Dugesia* coexist in many springs and streams in seven eastern Washington counties. Specifically, Lang has recorded *Polycelis coronata, Phagocata oregonensis* and *Dendrocoelopsis vaginata* at the following localities:

WHITMAN COUNTY
—numerous springs at north end of Rock Lake.

SPOKANE COUNTY
—spring in city of Cheney.
—spring and brook below Pine Lake.

ADAMS COUNTY
—spring and brook 8 km (5 miles) north of Washtucna.

In addition, Lang noted that *Dendrocoelopsis vaginata* and *Dugesia sp.* were found in a creek in Spokane County, 8.8 km (5.5 miles) north of Reardan. He also collected *Dendrocoelopsis vaginata* and *Polycelis coronata* together at a spring west of Spring Lakes in Lincoln County. Although I recorded virtually no instances of coexistence of freshwater triclads in western Washington, such coexistence is common in eastern Washington. The causes of this difference are extremely puzzling, and elucidation of environmental factors involved in the dichotomy would be a worthy topic for future ecological research.

Discussion

The question of sexuality in natural populations of triclad flatworms is extremely complex, and the factors involved in inducing sexual maturity are probably different in each species. Indeed, differences among populations of a single species may vary in this regard. Kenk (1972:22) indicated that in *Dugesia dorotocephala* some populations may rely completely upon asexual reproduction but in others sexual reproduction may prevail. This may be the case in the Washington populations of *D. tigrina* as well, seeing that in one Whatcom County population sexually mature individuals were observed while in another none were observed.

In Washington populations of *Polycelis*, sexually mature individuals were relatively rare in most cases, and no egg capsules or cocoons were observed. Kenk (1973a) noted that no capsules or cocoons have ever been observed in any of the North American species of *Polycelis* and that the factors involved in inducing sexuality are unknown. The effect of temperature on sexual maturity and other aspects of the life cycle in European triclads has been shown by various workers (Reynoldson, 1960; Reynoldson *et al.,* 1965; Taylor and Reynoldson, 1962) and may also be important in North American species. Indirect evidence regarding temperature may be seen in the Washington populations of *Polycelis* which were observed in habitats between 5 and 14C. However, in the 28 populations studied, sexually mature individuals were observed only in those habitats between 10 and 11C, a relatively narrow temperature range.

In the *Phagocata* population studied in Whatcom County, sexually mature individuals were never observed; reliance upon the asexual process of fragmentation may be caused by the short time period available during the year.

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Literature Cited

Ball, I. R., and C. H. Fernando. 1968. On the occurrence of *Polycelis* (Turbellaria, Tricladida) in western Canada. Canadian Field-Natur. 82: 213-216.

Beck, D. E. 1954. Distributional and natural history notes on *Polycelis coronata* (Girard) in Utah. Proc. Utah Acad. Sci. Arts Letters 31: 79-82.

Braithwaite, L. F. 1962. The taxonomic problem of *Polycelis* in the United States. Brigham Young Univ., Salt Lake City, M.S. thesis. 32 pp.

Carpenter, J. H. 1969. A new planarian from Utah, *Phagocata crenophila* n. sp. (Turbellaria, Tricladida). Trans. Am. Micros. Soc. 88: 274-281.

Castle, W. A. 1928. An experimental and histological study of the life-cycle of *Planaria velata.* J. Exp. Zool. 51: 417-483.

————, and L. H. Hyman. 1934. Observations on *Fonticola velata* (Stringer), including a description of the anatomy of the reproductive system. Trans. Am. Micros. Soc. 53: 154-171.

Chandler, C. M., and J. T. Darlington. 1975. A survey of the epigean planarians (Turbellaria, Tricladida, Paludicola) of New Mexico. Southwestern Naturalist 19: 387-394.

Darlington, J. T., and C. M. Chandler. 1972. A survey of the epigean triclad turbellarians of Tennessee. Amer. Midland Naturalist 88: 158-166.

Holmquist, C. 1967. *Dendrocoelopsis piriformis* (Turbellaria: Tricladida) and its parasites from northern Alaska. Archiv fur Hydrobiologie 62: 453-466.

Hyman, L. H. 1931. Studies on the morphology, taxonomy, and distribution of North American triclad turbellaria III. On *Polycelis coronata* (Girard). Trans. Am. Micros. Soc. 50: 124-135.

————. 1963. North American triclad turbellaria, 16: Fresh-water planarians from the vicinity of Portland, Oregon. Am. Mus. Novitates 2123: 1-5.

Kenk, R. 1935. Studies on Virginian triclads. J. Elisha Mitchell Scientific Soc. 51: 79-125.

————. 1944. The fresh-water triclads of Michigan. Misc. Publ. Mus. Zool. Univ. Mich. 60: 1-44.

————. 1952. Fresh-water triclads (Turbellaria) of the Rocky Mountain National Park region, Colorado. J. Wash. Acad. Sci. 42: 193-198.

————. 1953. The fresh-water triclads (Turbellaria) of Alaska. Proc. U.S. Nat. Mus. 103: 163-186.

————. 1972. Freshwater Planarians (Turbellaria) of North America. Biota of Freshwater Ecosystems, Identification Manual No. 1. Environmental Protection Agency. 81 pp.

————. 1973a. Freshwater triclads (Turbellaria) of North America, V: The genus *Polycelis.* Smith. Cont. Zool. 135: 1-15.

————. 1973b. Freshwater triclads (Turbellaria) of North America, VI: The genus *Dendrocoelopsis.* Smith. Cont. Zool. 138: 1-16.

Nixon, S. E. 1974. Some behavioral observations on a cave-dwelling planarian. J. Biol. Psych. 16: 32-33.

————. 1975. The ecology of Deadhorse Cave. Northw. Sci. 49: 65-70.

————. 1977. The ecology of freshwater flatworms in Washington. *In* Symposium on Terrestrial and Aquatic Ecological Studies of the Northwest, Cheney, Washington, March 1976, pp. 337-345.

Reynoldson, T. B. 1960. A quantitative study of the population biology of *Polycelis tenuis* (Ijima) (Turbellaria, Tricladida). Oikos 11: 125-141.

————, J. O. Young, and M. C. Taylor. 1965. The effect of temperature on the life-cycle of four species of lake-dwelling triclads. J. Animal Ecol. 34: 23-43.

Stringer, C. E. 1909. Notes on Nebraska turbellaria with descriptions of two new species. Zool. Anz. 34: 257-262.

Taylor, M. C., and T. B. Reynoldson. 1962. The population biology of lake-dwelling *Polycelis* species with special reference to *P. nigra* (Muller) (Turbellaria, Tricladida). J. Animal Ecol. 31: 273-291.

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Food Habits of Jumping Mice (Zapus trinotatus and Z. princeps) in Western North America

Abstract

Major foods of 69 western jumping mice, *Zapus princeps,* and 93 Pacific jumping mice, *Z. trinotatus,* were generally similar to those of meadow jumping mice, *Z. hudsonius.* Seeds, particularly grass seeds, and fruits, such as of *Rubus* and *Vaccinium,* were important, as was the fungus *Endogone.* Animal matter was less abundant than in *Z. hudsonius,* but the chief animal food in *Z. princeps* and *Z. trinotatus* was lepidopterous larva as in *Z. hudsonius.*

Introduction

Detailed studies have been presented of the food habits of jumping mice, *Zapus hudsonius* and *Napeaozapus insignis* from New York (Whitaker, 1963a, 1963b) and *Z. hudsonius* from Indiana (Whitaker and Mumford, 1971). There is scant information, however, concerning the foods of the western or Pacific jumping mice, *Z. princeps* or *Z. trinotatus,* although several papers refer in general terms to their diets. Some of these papers are cited here. Maser and Franklin (1974) stated that thimbleberry *(Rubus parviflorus),* salmonberry *(R. spectabilis),* evergreen huckleberry *(Vaccinium ovatum),* skunk cabbage *(Lysichitum americanum),* seeds, moss, and fungi were foods of *Z. trinotatus* in Oregon, and Maser (unpublished) found that blueleaf huckleberry *(Vaccinium deliciosum),* Himalayan blackberry *(Rubus procerus),* and stinking current *(Ribes bracteosum)* were utilized as foods in Oregon. Dalquest (1948) listed velvet grass *(Holcus lanatus),* grass seeds, dock *(Rumex),* skunk cabbage, and blackberries as foods of this species in Washington. Clark (1971) presented a general analysis of the foods of *Z. princeps* from Teton County, Wyoming. He found "seeds" to comprise the greatest quantity of the diet (82 percent volume, 100 percent frequency) followed by green vegetation and arthropods in trace amounts. Bailey (1930) found only "clean white starch" in *Z. princeps* which he examined from Yellowstone Park, Wyoming. Grass seeds were reported as foods by Armstrong (1972), Ingles (1965), Henshaw and Birdseye (1911), and Banfield (1974) from several localities. Banfield (1974) listed "summer berries." Whitaker (1962) reported small percentages of *Endogone* from the stomachs of *Z. princeps* from California, and Dowding (1955) reported *Endogone pulvinata* from this species in Alberta, Canada.

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The purpose of this paper is to present information on the food habits of *Z. trinotatus* and *Z. princeps* from western North America.

Methods and Materials

Jumping mice for this study were collected during two trips into western North America by Gwilym S. and Diana B. Jones in the summers of 1973 and 1974, and by Chris Maser during his work on mammals of the Oregon Coast (1970-1973). Stomach contents were examined with a 10 to 70 power, zoom dissecting microscope. Identifications were made by comparison with known items. Stomachs from *Zapus princeps* were examined from the following localities: British Columbia (26 stomachs, most from near Quesnel), Wyoming (21, most from Albany and Carbon Counties), California (11 from Nevada County), and Utah (11, most from Weber County). Stomachs from *Zapus trinotatus* were examined from the following localities: Oregon (43, from several counties), British Columbia (27, most from the Fraser River Valley near Hope), Washington (20, most from Mason County), and California (3 from Humboldt County).

Results and Discussion

Results of stomach analysis are presented for *Zapus trinotatus* (Table 1) and *Z. princeps* (Table 2). For comparison, some of the major foods of *Z. hudsonius* from New York (Whitaker, 1963a) were summarized. Since most of the present collections were in summer, *Z. hudsonius* data for July, August, and September were used, including 159, 138, and 191 stomachs respectively. Percentage volumes of major groups of foods for those months were grass seeds 36.4, 26.9, 30.8; other seeds 21.7, 28.5, and 23.3; *Endogone* 16.7, 15.1, 19.5; lepidopterous larvae 5.6, 6.5, 8.4; other animal foods 1.3, 2.1, 2.8; and fleshy fruits *(Fragaria, Vaccinium, Rubus,* and *Viburnum)* 4.6, 7.6, and 5.7.

There are great similarities between the food habits of eastern and western jumping mice. Seeds, particularly grass seeds, are the predominant food. Seed content in the stomachs of *Z. trinotatus* ranged from 49.6 to 56.6 percent of the total volume, and in *Z. princeps* it ranged from 28.8 to 52.3 percent. These are similar to the values from New York (54.1 to 58.1 percent). Grass seeds ranged from 33.8 to 46.7 in *Z. trinotatus,* 9.5 to 62.1 in *Z. princeps* and 26.9 to 36.4 in *Z. hudsonius.*

The second major group of foods eaten by North American zapodids consists of subterranean fungi, particularly *Endogone. Endogone* ranged from 5.5 to 19.9 percent volume in *Z. trinotatus,* 1.4 to 17.7 in *Z. princeps,* and 15.1 to 19.5 in *Z. hudsonius.* Odors emitted by the maturing sporocarps allow the mice to detect and dig out the hypogeous fungi. In eastern *Z. hudsonius, Endogone* is usually found in greater abundance in individuals from more moist situations. (Whitaker, 1962, 1963a), but we have too little information to determine the relationship of this food to habitat of western or Pacific *Zapus.*

Animal materials, chiefly lepidopterous larva, were eaten at rates of 6.9, 8.6, and 11.2 percent in the summer by *Z. hudsonius.* Animal materials were utilized slightly less in this sample of *Z. trinotatus,* with values ranging from 3.5 to 6.3 percent volume. In *Z. princeps* from British Columbia and Wyoming, animal foods totaled only 0.8 and 3.8 percent of the volume respectively. However, in those from California and Utah they were 13.7 and 45.1 respectively. Local abundance of larvae and other insects probably influenced the values in these small samples.

TABLE 1. Food from 43 stomachs of *Zapus trinotatus* from Oregon, 3 from California, 20 from Washington, and 27 from British Columbia.

	Oregon & California		British Columbia		Washington	
	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Grass seeds	37.5	73.9	46.7	92.6	33.8	90.0
Rubus spectabilis Salmonberry	15.0	28.3	0.1	3.7	10.4	35.0
Unidentified seeds	10.5	23.9	2.9	11.1	5.1	40.0
Starchy material	9.3	13.0	3.7	3.7	—	—
Endogone	6.1	30.4	5.5	51.9	19.9	70.0
Lepidopterous larvae	5.0	45.7	4.0	18.5	2.5	20.0
Vaccinium parviflorum Red Huckleberry	3.9	6.5	—	—	1.5	5.0
Cerastium seeds	3.5	10.9	trace	7.4	17.6	60.0
Unidentified vegetation	3.1	28.3	3.9	44.0	5.0	55.5
Unidentified fungi	1.7	15.2	trace	3.7	2.8	20.0
Lonicera involucrata Twinberry	1.5	2.2	1.8	22.2	—	—
Unidentified insect	1.0	19.6	0.4	18.5	0.8	20.0
Gaultheria shallon seeds Salal	0.8	6.5	—	—	0.1	5.0
Rubus sp.	0.4	2.2	—	—	0.1	5.0
Formicidae	0.2	4.3	—	—	—	—
Unidentified animal	0.1	2.2	—	—	0.2	10.0
Rumex seeds	0.1	4.3	trace	3.7	—	—
Aphididae	trace	2.2	trace	3.7	—	—
Moss	—	—	0.2	3.7	0.5	5.0
Rubus parviflorus Thimbleberry	—	—	30.6	59.3	—	—
Mites	—	—	0.1	7.4	—	—
Coleoptera	—	—	trace	3.7	—	—
	99.7	.	99.9	.	100.3	.

The last major category of foods eaten by zapodids is that of the fleshy fruits, such as those of *Vaccinium* or *Rubus*. Fruits, heavily utilized by North American zapodids, are likely preferred over many types of foods, as they are generally consumed when available. Some fruits are available for only a short period, but may form a major proportion of the diet at that time. The kinds of fruit vary. In the east, major fruits are the strawberry *(Fragaria virginiana)*, the various blackberries and raspberries (*Rubus* spp.), the blueberries (*Vaccinium* spp.), and the fruit of arrowwood *(Viburnum dentatum)*. In the west, the fruits of *Rubus* and *Vaccinium* are again eaten, particularly salmonberry *(R. spectabilis)*, thimbleberry *(R. parviflorus)*, and red huckleberry *(Vaccinium parviflorum)*. Salmonberry was the major food in a series of stomachs examined from *Z. princeps* from British Columbia, and also in *Z. trinotatus* from Oregon, California, and Washington. *Vaccinium* and other fruit presently unidentified were also important. Fruit of thimbleberry (actually mostly seeds in this case) was important in the *Z. trinotatus* sample from British Columbia. The fruits of both salmonberry and thimbleberry fall to the ground when mature and are readily available to the mice. The mice obtain some berries, such as those of salal *(Gaultheria shallon)*, by climbing into the low bushes.

Food habits of North American mice of the genus *Zapus* are similar in that the various species feed on the same four major groups of foods. The group listed in

approximate order of decreasing use are: seeds, particularly grass seeds, subterranean fungi of the genus *Endogone,* animal materials, particularly lepidopterous larvae, and fleshy fruits, varying with locality.

TABLE 2. Food from 26 stomachs of *Zapus princeps* from British Columbia, 11 from California, 21 from Wyoming, and 11 from Utah.

	British Columbia		California		Wyoming		Utah	
	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Rubus spectabilis Salmonberry	27.8	42.3	—	—	—	—	—	—
Grass seeds	23.1	50.0	45.9	54.5	62.1	80.1	9.5	18.2
Endogone	12.9	46.2	17.7	54.5	9.1	28.6	1.4	9.1
Vaccinium	10.4	23.1	—	—	0.7	4.8	—	—
Unidentified vegetation	9.8	53.9	5.0	27.3	5.2	38.1	2.7	18.2
Unidentified fruit	8.7	19.2	—	—	—	—	—	—
Unidentified seeds	5.6	19.2	6.4	36.4	6.1	23.8	41.4	90.9
Unidentified fungi	1.0	3.8	5.5	9.1	2.9	9.5	—	—
Lepidopterous larvae	0.6	7.7	10.0	27.3	0.5	4.8	42.3	81.8
Scarabaeidae	0.2	3.8	—	—	—	—	0.9	9.1
Cerastium seeds	0.1	3.8	—	—	5.5	14.3	—	—
Starchy material	—	—	5.0	18.2	4.5	4.8	—	—
Unidentified insect	—	—	2.3	27.3	1.2	9.5	0.5	9.1
Carabidae	—	—	1.4	9.1	—	—	—	—
Rubus sp.	—	—	0.9	9.1	—	—	—	—
Coleoptera	—	—	—	—	1.4	4.8	—	—
Diptera	—	—	—	—	0.7	4.8	—	—
Chrysomelid larvae	—	—	—	—	—	—	0.9	9.1
Formicidae	—	—	—	—	—	—	0.5	9.1
TOTAL	100.2		100.1		99.9		100.1	

Literature Cited

Armstrong, D. M. 1972. Distribution of Mammals in Colorado. Monograph, Mus. Nat. Univ. Kansas 3: 415 pp.

Bailey, V. 1930. Animal Life of Yellowstone National Park. C. C. Thomas, Publ., Baltimore. 231 pp.

Banfield, A. W. F. 1974. The Mammals of Canada. Univ. Toronto Press, Toronto, 438 pp.

Clark, T. W. 1971. Ecology of the western jumping mouse in Grand Teton National Park, Wyoming, Northw. Sci. 45: 229-238.

Dalquest, W. W. 1948. Mammals of Washington, Univ. Kansas Publ., Mus. Nat. Hist. 2: 1-144.

Dowding, E. S. 1955. *Endogone* in Canadian rodents. Mycologia 47: 51-57.

Henshaw, H. W., and C. Birdseye. 1911. The Mammals of Bitterroot Valley, Montana, in Their Relation to Spotted Fever. U.S. Dept. Agric., Bur. Biol. Surv. Circ., 82: 24 pp.

Ingles, L. G. 1965. Mammals of the Pacific States. Stanford Univ. Press, Stanford, Calif. 506 pp.

Maser, C., and J. F. Franklin. 1974. Checklist of Vertebrate Animals of the Cascade Head Experimental Forest. USDA Forest Serv. Res. Bull., PNW-51: 32 pp.

Whitaker, J. O., Jr. 1962. *Endogone, Hymenogaster* and *Melanogaster* as small mammal foods. Amer. Midl. Nat. 67: 152-156.

————. 1963a. A study of the meadow jumping mouse, *Zapus hudsonius* (Zimmermann) in central New York. Ecol. Monogr. 33: 215-254.

————. 1963b. Food, habitat and parasites of the woodland jumping mouse in central New York. J. Mammal., 44: 316-321.

————, and R. E. Mumford. 1971. Jumping mice (Zapodidae) in Indiana. Proc. Indiana Acad. Sci., 80: 201-209.

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Avifaunal Survey of the Trojan Nuclear Power Station[1]

Abstract

A walking path was established that entered or passed the important bird habitats present on the undeveloped property surrounding the Trojan Nuclear Power Station in Oregon. Ten early morning walks were made at approximately one month intervals in 1973. All identifiable birds were counted. Seventy-eight species were recorded from the path. If faithfully conducted over a period of years, the bird path method of avifaunal censusing can be expected to detect at least gross changes in bird populations as related to changing land use patterns.

Introduction

The National Environmental Policy Act (NEPA) of 1969 has created a need for providing written statements to evaluate the environmental impacts of construction and operation of nuclear power stations and other kinds of industrial facilities. Birds usually inhabit sites potentially suitable for nuclear power stations and are an important consideration because certain species are regarded as rare, threatened, or endangered. Others are commercially and recreationally valuable.

One of the important questions is: How much of an effort needs to be made to comply fully with the intent of NEPA? Probably the most extensive effort made towards evaluating impact assessments so far is that associated with nuclear power station siting and the United States Nuclear Regulatory Commission (Eberhardt, 1976).

This paper reports the results of an avifaunal survey made prior to the operation of the Trojan nuclear power station.

The Site

The Trojan nuclear power station is located on a 600-acre site near Prescott, Columbia County, Oregon. The land is mostly undeveloped and is occupied by forest communities. The forests are interrupted by small hay meadows, freshwater ponds, and grassy marshes. The dominant trees are Douglas-fir, *Pseudotsuga menziesii,* growing on the upland soils; and black cottonwood, *Populus trichocarpa,* and Oregon ash, *Fraxinus latifolia,* growing on lowland soils.

Methods

Prior experience as to the kind of information and detail needed to provide data to assess the long-term impact of power station operations on bird populations was lack-

[1] This study was funded by the Portland General Electric Company, Portland, Oregon.

ing. Thus, an arbitrary decision was made to establish a survey path to be followed once each month and to record all birds seen along this path. The path was walked in the early morning hours and was approximately 2.5 miles long (Fig. 1). The path penetrated conifer forest and deciduous tree communities, skirted the edges of marsh

Figure 1. Aerial photograph of the Trojan nuclear power station. The dotted line shows the bird survey path. The path begins at the upper (northern) property boundary and terminates near the prominent cooling tower structure. The rectangular reflection pond west of the cooling tower is approximately 1500 feet in length. (PNL 766-075-1)

and pond habitats, and forest and meadow edges. When in forest stands, the line of sight was often restricted to a few yards, but in open areas line of sight would extend to ½ mile or more.

An aerial photograph (Fig. 1) was taken to provide a record of the extent of plant communities and to serve as an indicator of future changes in communities, such as clear-cut logging or other events that could alter the species composition and relative abundance of birds along the path. In all, 10 visits were made at about 1-month intervals.

Bird identifications were made with the aid of binoculars, but it was not always possible to identify all birds seen, especially those in heavy cover. Unidentified birds were not included in the species lists.

Results

Upland game birds were not abundant at the Trojan site even though five species were represented (Table 1). Birds reared on the site property can easily cross boundaries where they could be shot during the hunting season even though hunting is not permitted on the site property.

TABLE 1. Birds counted along an established survey path at the Trojan Power Station Site, 1973.

Common Name	J	F*	M	A	M	J	J	A	S	O	N*	D
Upland Game Birds												
Ruffed Grouse									1			1
Mountain Quail								9	7			
Mourning Dove							2					
Ring-necked Pheasant										1		
Band-tailed Pigeon							2					
Waterfowl												
Mallard Duck			11	10	10	3	16	15	18	∿200		21
Wood Duck					6		1		1			
American Coot	1									10		29
American Wigeon	75		45									
Canada Goose	50											42
American Merganser	9		2									
Hooded Merganser					10							
Green-winged Teal										13		
Pintail										2		
Hawks and Vultures												
Red-tailed Hawk	2		1	4		2	2	1	1			1
Turkey Vulture				1				1				
Gulls and Shorebirds												
Great Blue Heron	2		1	3	10	8	3	17	2	4		1
Killdeer			2	2		3	1	1	1	12		
Spotted Sandpiper					3	4	2	2				
Ring-billed Gull	∿240				2							
Western Sandpiper								3				
Lesser Yellowlegs								2				
Herring Gull				10								
Black-crowned Night Heron								2				
Perching Birds												
Black-capped Chickadee	8		10	12	2	6	2	10	10	29		15
Song Sparrow	15		8	7	10	6	8	8	22	13		17
Robin			8	2	8	3	4	4	4	5		1
Steller's Jay	1		5	1	4	2	2	3				7
Red-winged Blackbird			1	10	15	10	5		∿150	10		3
Winter Wren	1		3	4	2	1		4		9		3
Rufous-sided Towhee	1		1	2	2	3	6					4
Dark-eyed Junco	40		6	1	2			6				57

TABLE 1. (Continued)

American Goldfinch		2	10	10	15	≈100			
Purple Finch				3	8	2	2	4	
Common Flicker	2		1		2	1	1		
Chestnut-backed Chickadee			1		6	14		26	2
Rough-winged Swallow			6	6	6	≈100	∞		
Barn Swallow			20	9	8	60	∞		
Long-billed Marsh Wren		4	2					2	4
Common Crow		3	2	2				1	
Starling			1	15	8		4		
White-crowned Sparrow	1				5	6	1		
Common Bushtit		1	1		1	1			
Violet-green Swallow				12	8	60	∞		
Pine Siskin			4		8	10			
Yellowthroat		3	2	1					
Hermit Thrush				6	2	1			
Bewick's Wren		2		4	4				
Brown-headed Cowbird			4	10	18				
Ruby-crowned Kinglet	2		1					1	1
Northern Oriole			4	4	4				
Golden-crowned Kinglet				3				21	54
Orange-crowned Warbler		2	1		2				
Hammond's Flycatcher			2	1	4				
Olive-sided Flycatcher			2		3	1			
Downy Woodpecker							1		1
Cliff Swallow			20	8					
Tree Swallow		8	30						
Cedar Waxwing				1	2				
Savannah Sparrow					16	2			
Black-headed Grosbeak				3	3				
Rufous Hummingbird		2			1				
Western Tanager					2		1		
Hutton's Vireo							1		1
Alder Flycatcher				4	2				
Trail's Flycatcher		3	4						
Hairy Woodpecker						2	1		
Warbling Vireo		1							
Black-throated Gray Warbler						3			
Yellow-rumped Warbler		8							
Yellow-bellied Sapsucker				1					
Williamson's Sapsucker								1	
Brewer's Blackbird							1		
House Finch									1
Varied Thrush									2
Brown Creeper								4	
White-throated Sparrow								1	
Fox Sparrow									5

Birds observed on the site but not along the established pathway: Pied-billed Grebe, Whistling Swan, Cinnamon Teal, Blue-winged Teal, Ring-necked Duck, Goshawk, American Kestrel, Common Snipe, Great Horned Owl, Calliope Hummingbird, Belted Kingfisher, Pileated Woodpecker, Western Wood Pewee, Bank Swallow, Purple Martin, Scrubjay, Water Pipit, Yellow Warbler, MacGillivray's Warbler, Wilson's Warbler, and House Sparrow.

*=No observations made

Ducks and geese were much more numerous than upland game birds, especially in the autumn months when migrant birds fed and rested on the ponds. The species recorded during this season were similar to those reported on public shooting grounds on Sauvie Island (Oregon Dept. of Fish and Wildlife, 1975). The ponds were not great producers of ducks, although a few broods of mallards and wood ducks were raised (Table 1). Mallards and wood ducks are reported as the principal nesting ducks in Columbia County (Oregon Dept. of Fish and Wildlife, 1975).

Predatory birds were scarce. The most often sighted raptor was the red-tailed hawk (Table 1). The great blue heron was abundant, having been seen on every visit, and 17 individuals were counted during one survey. These birds do not nest on the Trojan property, but a large nesting colony is reported from Bachelor Island located in the Columbia River upstream from the Trojan property.

The diversity of habitats at the Trojan site is mainly responsible for the variety of bird species. Seventy-eight species were recorded from the census path and twenty-one additional species were identified during the course of other biological studies on the site property (Table 1).

There were no rare, threatened, or endangered species observed during the course of field observations, although the whistling swan is protected from hunting kills in Oregon (U.S. Dept. of Interior, 1973; Marshall, 1969).

Discussion

The purpose of avian surveys at nuclear power station sites is to establish whether rare, threatened, or endangered species occur on the property and, if so, to determine if their existence would be threatened by construction and operation of the site. Another purpose is to determine if common, commercially, or recreationally valuable bird populations would be seriously affected by construction and operation of the station.

Nuclear power stations, like other kinds of massive building complexes, pre-empt natural avian habitats. Unlike many other kinds of industrial complexes, nuclear power stations are sited with a large buffer zone of undeveloped land around the buildings. The acreage varies, but 1,000 acres is probably fairly representative. The land use in the buffer zone varies according to site, but human residences are not permitted.

Depending on future land use priorities, the buffer zone lands can provide habitat for birds for the life of the nuclear station, *i.e.,* 30-40 years, in a zone in which wildlife habitats could dwindle with the development of housing, agriculture, or other industrial facilities.

The anticipated proliferation of nuclear power stations in the United States has increased public concern as to the deleterious potential for nuclear power station operation on wild bird populations, and this concern has prompted Mellinger and Schultz (1975) to review the literature involving wild birds and ionizing radiation. The normal operation of a modern nuclear power station is expected to release only small amounts of radionuclides into the surrounding atmosphere. Low level atmospheric releases are expected to produce ecological effects that would be inseparable from those produced by an array of concomitant environmental stresses. Some bird mortality may result from collisions with buildings, towers, and other structures such as transmission lines. This kind of mortality can be ascertained by observing if dead birds are

found at the bases of the structures. To date, there has been no bird mortality as a result from collisions with buildings, the cooling tower, or other man-made structures on the Trojan site. Eberhardt (1976) reviewed environmental statements prepared for 15 nuclear stations in the United States in terms of their contributions to quantitative ecological methods and concluded that the limitations of animal census methods and substantial variability make it doubtful that anything less than gross population changes can be detected in the usual sequence of pre- and post-operational ecological observations.

The bird path survey has some advantages over the plot census technique as employed by Anderson (1973). It is less time-consuming and permits coverage of more habitats. The bird path survey is expected to detect at least gross changes in species composition and abundance. The major disadvantage is that population density (*i.e.,* individuals per unit area) is not obtainable. Density data are essential if comparison between different habitats and regions is to be made, but they are not so important if each nuclear power station site is treated individually.

A bird path survey was conducted on a riparian tree-shrub community in south-central Washington and seemed to assess adequately changes in avian populations after a 10-year time lapse (Rickard and Rickard, 1972).

Although bird populations are more amenable to census methodologies than most other kinds of wild vertebrates, and considerable time and effort have been expended to elucidate ecological principles in northwestern forest communities (e.g., Wiens and Nussbaum, 1975; Anderson, 1972), the bird path census appears adequate for nuclear power plant impact assessment, particularly if done faithfully, frequently, and in conjunction with knowledge of changing plant community patterns as indicated by changing land uses and on-going radiological surveillance programs.

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Literature Cited

Anderson, S. H. 1972. Seasonal variation in forest birds of western Oregon. Northw. Sci. 46: 194-206.

Eberhardt, L. L. 1976. Quantitative ecology and impact assessment. J. of Environ. Manage. 4: 27-70.

Marshall, David B. 1969. Endangered Plants and Animals of Oregon, Special Report 278. Agricultural Experiment Station, Oregon State University, Corvallis, Oregon. 23 pp.

Mellinger, P. J., and V. Schultz. 1975. Ionizing radiation and wild birds. A review: CRC Critical Reviews in Environmental Control 5: 397-421.

Oregon Department of Fish and Wildlife. 1975. 1975 Annual Report—Wildlife Division. Portland, Oregon. 178 pp.

Rickard, W. H., and B. J. Rickard. 1972. A comparison of winter bird populations after a decade. The Murrelet 53: 42-47.

United State Department of Interior. 1973. Threatened Wildlife of the United States. U.S. Government Printing Office, Washington, D.C. 289 pp.

Wiens, J. A., and R. A. Nussbaum. 1975. Model estimation of energy flow in northwestern coniferous forest bird communities. Ecology 56: 547-561.

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A Study of Climax Western Redcedar (Thuja plicata Donn.) Forest Communities in the Selway-Bitterroot Wilderness, Idaho

Abstract

Old-growth *Thuja plicata* forest communities occurring in the Selway-Bitterroot Wilderness in northern Idaho were the subject of investigation. It is within this wilderness that western redcedar reaches its southeastern range limits in Idaho. Mature, climax cedar groves sampled in both lower and upper drainage segments indicate that only the stands at higher elevations are reproducing themselves at this time. Lower cedar groves have well-developed overstories, but lack reproduction. The lower cedar groves may be experiencing stress in consequence of lower moisture at its range limits and are incapable of reproducing successfully. A hypothesis is presented that high wildlife populations in the past depleted the cedar reproduction, and this depletion effectively inhibited vegetative propagation of the redcedar.

Introduction

Some of northern Idaho's most spectacular, surviving examples of old-growth western redcedar *(Thuja plicata)* groves and other old-growth forest composed of redcedar and grand fir *(Abies grandis)* exist within the central portion of the half-million hectare (1.2 million acres) Selway-Bitterroot Wilderness (46° 00′ N, 115° 00′ W, Fig. 1). Redcedar grove communities, 400 to 500 years old, are common on the streamside flats and lower terraces of Moose Creek, Bear Creek, and other tributaries of the upper Selway River.

Very little scientific study has been made of these particular wilderness forests. Although the entire Selway-Bitterroot Wilderness is well within the designed "core area" reportedly investigated by Daubenmire (1952) and by Daubenmire and Daubenmire (1968, see their Fig. 1), it has become apparent that very little, if any, of the roadless wilderness portion of their study area was in fact examined or data collections made (Daubenmire and Daubenmire, 1968, Appendix B: stand locations) in this wilderness. Current vegetation studies, partially reported here, have been pursued during a five-summer period between 1971 and 1975.

By omitting data collection within this part of northern Idaho, the Daubenmires (1968) failed to give recognition to several special phenomena that occur in the Selway-Bitterroot Wilderness particularly associated with redcedar-grand fir communities. It is within this wilderness portion of Idaho that *Thuja plicata* reaches its southeastern range limits. It has been noted in these current studies that as redcedar approaches its range limits, its ecological behavior and competitive interactions with its close associate, grand fir, are altered. In some portions of the wilderness old-aged redcedar stands are showing no evidence of reproducing themselves, whereas elsewhere the cedar is reproducing very successfully.

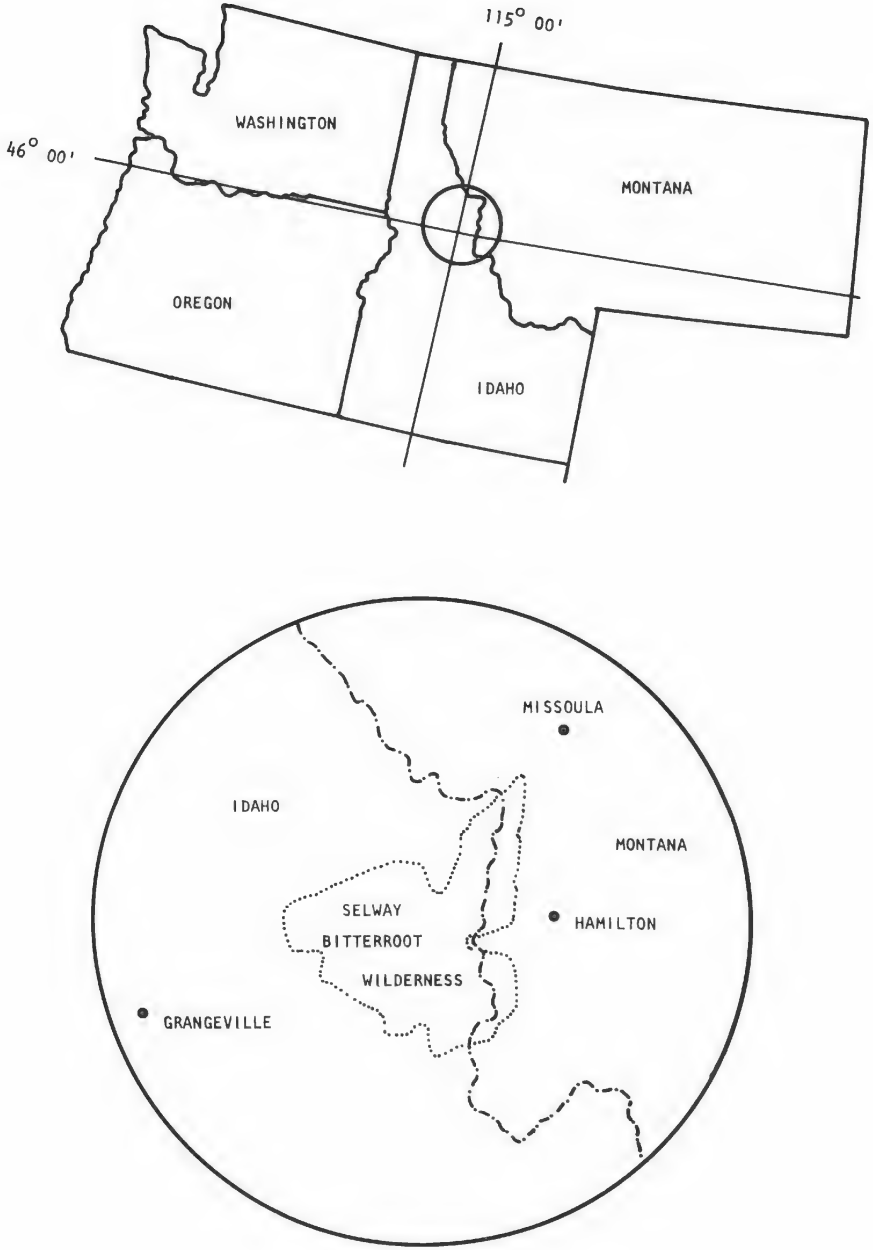

Figure 1. Location Maps of the Selway-Bitterroot Wilderness in northern Idaho.

It is the objective of this paper to present field data collected from a series of old-growth redcedar-grand fir communities that will provide an insight into the current status of climax *Thuja plicata* forests within this part of the cedar's botanical range. An interpretation of these data should contribute to a better understanding of the problems that have been experienced in applying habitat type classification developed by the Daubenmires (1968) to redcedar-grand fir communities in this portion of their core area (Steele, Arno, and Pfister, 1976).

Phytogeographical Features

Daubenmire has described and discussed in detail the occurrence of Pacific Coastal floristic elements in northern Idaho (1943, 1952, 1969). In addition, Little (1971) has provided a detailed atlas of Pacific Northwest tree distributions, and the eastward extensions into northern Idaho of such species as western redcedar, grand fir, western whitepine *(Pinus monticola)*, western hemlock *(Tsuga heterophylla)*, western yew *(Taxus brevifolia)* and others are well documented. The available literature on tree distribution patterns in northern Idaho clearly reveals that the Selway-Bitterroot Wilderness lies within a key phytogeographical zone.

It is within the region bounded by the Lochsa River to the north and the Salmon-Clearwater River divide to the south that several of the major coastal tree species reach their southeastern range limits. Western larch and western whitepine both occur just within the northern edge of the wilderness but exist only as scattered small populations or isolated individuals. Redcedar is common along the major stream courses within the northern half of the wilderness but becomes less common farther south; it reaches its southern limits in the vicinity of the upper reaches of the Selway River. Western hemlock, a common associate of redcedar north of the Lochsa River, has not been seen within the wilderness.

Grand fir, in contrast, extends well southward from the wilderness, and reaches its range limits in portions of central Idaho. With other coastal species reaching their range limits, grand fir exhibits an expansive distribution in the wilderness area and adjacent parts of the Nezperce National Forest. Grand fir without question is the most widely distributed species on the Selway River drainage; it occupies warm aspects at elevations below 600 m, mingling with formerly fire-maintained ponderosa pine *(Pinus ponderosa)* savannahs, as well as forming mixtures with subalpine fir *(Abies lasiocarpa)* and Engelmann spruce *(Picea engelmannii)* at elevations up to 1,800 m. As a consequence of grand fir's behavior, a Douglas-fir *(Pseudotsuga menziesii)* forest zone is poorly and incompletely developed within much of the wilderness.

Description of the Study Area

Detailed destriptions of the basic geography, geology, and climatic features of the Selway-Bitterroot Wilderness have been published elsewhere (Leiberg, 1900; Lindgren, 1904; Habeck, 1972, 1976; Greenwood and Morrison, 1973; Finklin, 1974). In general, the wilderness is characterized by steep, mountainous terrain, with local relief between streamsides and ridgetops often 1000 to 1500 m. The highest elevations (about 3000 m) occur on the eastern boundary (Bitterroot Mountains), while the lowest altitudes (about 550 m) are found on the northwestern corner along the lower Lochsa River.

Annual moisture is well correlated with an east-west gradient, with local modifica-

tions induced by the terrain features. Western areas receive about 900 mm per year, and the upper slopes of the Bitterroot Mountains receive 1500 mm annually, much of it in the form of snow. Summer (July-August) temperatures at highest elevations average 16C, lower areas 22C; January temperatures range from –8C in the eastern mountains, to –2C in the lower western section of the wilderness.

The July-August period is typically warm and dry; it is during this period that summer lightning storms are common and the cause of wildfire ignitions (Habeck, 1972, 1976). Past fires have burned streamside redcedar-grand fir forests, but not with the same frequency as upland forests. Only rarely has it been noted that fires on adjacent upland slopes have spread into the moist cedar groves. Lightning often causes ignitions within the groves, but generally these have not led to widespread burning within the groves.

Since catastrophic wildfire occurs so infrequently in the streamside cedar forests, time allows the development of stands that are four or more centuries old. It is these climax forests that are given particular attention in this report.

Methods

The study of old-growth red-cedar fir forests in the Selway-Bitterroot Wilderness has been a part of a larger fire ecology study (Habeck, 1976) wherein stand samples were taken within all forest zones, and form a wide variety of successional stands in each zone. Forest stand structure in these studies was documented by utilizing a reconnaissance plot technique as described by Steele *et al.* (1975). Communities selected for structural and compositional characterization were examined closely and a 375 m^2 circular plot was positioned in a location considered typical for the entire stand. Within this plot all trees over 1.4 m in height were tallied by diameter size classes. Trees less than 1.4 m in height were tallied within a central 50 m^2 subplot; these tree counts were then converted to numbers per 375 m^2.

An estimate was made of the canopy coverage (Daubenmire, 1959) for each tree species, in each of three diameter classes, *viz.,* over 3 dm dbh, 1-3 dm dbh and under 1 dm dbh. Seven coverage classes were employed: T = 0-1 percent, 1 = 1-5 percent, 2 = 5-25 percent, 3 = 25-50 percent, 4 = 50-75 percent, 5 = 75-95 percent, and 6 = 95-100 percent. In calculating average cover percentages, the mid-points were used, *viz.,* 0.5 percent, 3.0 percent, 15.0 percent, 37.5 percent, 62.5 percent, 85.0 percent, and 97.5 percent.

The vascular understory species within the 375 m^2 plots were also assigned coverage values using the same scale used for the trees. Shrubs, ferns, and other forbs observed within the stand, but not occurring within it, were separately recorded as present. The nomenclature used follows Hitchcock and Cronquist (1973).

Stand aging did not prove to be a simple matter. Both *Thuja plicata* and *Abies grandis* exhibit decay within the heartwood (species of *Poria* and *Fomes* on redcedar, and *Echinodontium tinctorium* on grand fir). Heart rot destroys the inner growth rings, making precise aging impossible. An estimated age was extrapolated by counting rings within the sound wood, and then relating these to total stem diameter.

Results

In the course of sampling, a total of 84 stands were examined in detail. These occupy sites that range in elevation from 618 m to 1690 m (2040 to 5590 ft.). Stand ages

range from 22 to approximately 600 years. Only those stands over 300 years of age are considered here. Stands of this age support only a few surviving seral species, mostly Douglas-fir and ponderosa pine. The stand structure of these old-growth forests involves redcedar and grand fir, and a comparison of the two species was a major objective of this study.

One of the most clear-cut influences on cedar population dynamics involves elevation. By simply hiking elevational transects along stream courses, one is impressed by the gradual shift that takes place in the reproductive success of redcedar. At elevations below 1000 m, cedar appears to be doing very poorly, whereas at altitudes above 1000 m, within the same drainage system, the redcedar is reproducing itself as successfully as observed anywhere else in northern Idaho or northwestern Montana.

The basic nature of this elevational shift can be interpreted readily from the data summarized in Tables 1 and 2. In Table 1, a representative group of old-growth communities occurring at elevations below 870 m are summarized; Table 2 provides a similar compilation for a group of stands occurring at elevations above 1100 m.

The common feature seen in the stands existing at lower drainage positions is the absence of redcedar reproduction (trees smaller than 1 dm dbh) even though a well-developed overstory of cedar exists in each case. Grand fir is generally well represented in these lower stands, with stand 11 an exception. Grand fir does not display the longevity or have the ultimate growth potential of redcedar, and finding grand firs over 8 dm dbh is a rare event. None of the redcedar stands sampled by the Daubenmires

TABLE 1. Tree population analysis for a series of lower drainage cedar stands. The number of individuals of *Thuja plicata* (Thpl) and *Abies grandis* (Abgr) occurring within 375 m^2 plots is presented, distributed within diameter size classes.

Stand No. Stand Age Elevation	Species	Seedlings Below 1.4 m ht.	Diameter Classes (dm at dbh), Trees Over 1.4 m ht.									
			0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	>10
6	Thpl			2		1		1			1		
450 yrs	Abgr		6	12	3		2		1	1	1		2
690 m													
11	Thpl												5
600 yrs	Abgr				3								
717 m													
14	Thpl			1	3		3	3	1	2			
315 yrs	Abgr	45	6	4	4	1			1	1			
717 m													
19	Thpl			2	5	2	1		1	6	2		
400 yrs	Abgr	15	4	3	9	5							
733 m													
56	Thpl							1	4	2			
350 yrs	Abgr	60	3	4	2	2	1	1					
760 m													
20	Thpl				3	3		4	2	3		2	
420 yrs	Abgr	56	10	6									
760 m													
17	Thpl			1	2			2	1		2		1
450 yrs	Abgr	23	11	4	3	1	2	1					
780 m													

TABLE 2. Tree population analysis for a series of upper drainage cedar stands. The data are arranged as in Table 1.

Stand No. Stand Age Elevation	Species	Seedlings Below 1.4 m ht.	Diameter Classes (dm at dbh), Trees Over 1.4 m ht.									
			0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	>10
180 325 yrs 1106 m	Thpl	29	17	5	2	2	1			1			
	Abgr	37	5										
51 500 yrs 1133 m	Thpl	127	5	4	1		1	1					1
	Abgr	175	6	4	2	2				2			1
23 500 yrs 1140 m	Thpl	45	9			2	1		2	1		2	3
	Abgr	15	4										
24 475 yrs 1150 m	Thpl	97	7	1	2	1	1					1	2
	Abgr									1	1		
50 425 yrs 1150 m	Thpl	440	21	5	2	2	2	5	1		1		
	Abgr	172	15										
57 400 yrs 1217 m	Thpl	180	11	2	2	1	1		2	3			
	Abgr	32	3	1	1								
121 385 yrs 1480 m	Thpl	22	6	2	2	2		2	1	1			
	Abgr	15	1	5			1			1			

(1968, p. 63, *Thuja/Pachistima* habitat type) display this sort of population structure, and only one out of ten of their old-aged stands shows a similar sort of reproductive failure by redcedar.

In contrast, the climax redcedar forests occurring in upper drainage sites above 1000 m (Table 2) exhibit excellent reproductive success. Grand fir is present in all stands, and it also is reproducing successfully in most of these cedar stands. It is these higher stands that show a greater degree of similarity to the stands sampled by the Daubenmires (1968); it may be significant that nearly all of their samples of this community type occur at elevations over 1000 m.

The differences in reproductive success of redcedar in lower and upper drainage sites within the Selway-Bitterroot Wilderness are further emphasized in the data summarized for 29 climax stands in Table 3. Here average canopy cover percentages for redcedar and grand fir within three diameter size classes are provided. There are only minor differences in the average canopy cover among old, larger redcedars over 3 dm dbh in upper and lower drainage positions. The higher cedar communities, however, have cover values that are three times larger for intermediate-size trees (1-3 dm dbh), and about 40 times greater cover for cedar reproduction in the smallest diameter class.

Canopy coverage of grand fir is generally greater among the lower drainage stands, considering the mature trees only; it can be determined from the data in Tables 1 and 2 that the average number of grand fir reaching or exceeding diameters of 3 dm dbh is greater among the low elevation communities. Grand fir reproduction, however, is

TABLE 3. Comparison of average cover percentages, by diameter size classes, for *Thuja plicata* and *Abies grandis* occurring within two series of old-growth, streamside stands. Group A below occur below 1000 m, and have an average age of 430 years; group B occur above 1000 m and average 445 years.

Species: Diameter Size Classes		Cover Percentages Group A (n=14)	Group B (n=15)
Thuja plicata:	Over 3 dm dbh	55.7%	53.2%
	1-3 dm dbh	4.1	14.2
	Under 1 dm dbh	0.6	24.7
Abies grandis:	Over 3 dm dbh	10.8%	2.4%
	1-3 dm dbh	16.4	6.0
	Under 1 dm dbh	5.7	11.7

more dense at higher elevations.

Table 4 provides a list of the major understory species encountered in the 14 plot samples included in Tables 1 and 2. Cover class values are entered in this table, and it is evident that many of the understory plants have similar levels of occurrence and ranges of variation from plot to plot in both upper and lower stand groups. Among the 28 species listed, only *Clintonia uniflora* and *Coptis occidentalis* are found in all stands; they also have rather consistently high cover values. None of the 14 plots support all of the species; stand 121 has the lowest diversity (16 species), while stand 57 exhibits 24 of the species listed.

Eight of the understory species appear to have differential distribution patterns between the two stand groups. *Lonicera ciliosa* and *Spiraea betulifolia* are confined to lower drainage sites; *Menziesia ferruginea, Taxus brevifolia, Xerophyllum tenax, Athyrium filix-femina, Gymnocarpium dryopteris* and *Pyrola asarifolia* show a preference for higher drainage sites.

Perhaps because the forest communities being discussed here occur at or near the range limits of *Thuja plicata,* difficulties are experienced when an attempt is made to apply the Daubenmires' (1968) habitat typing classification to the stands summarized in Tables 1-4. Although the stands in Table 1, at lower drainage stations, might comprise exceptional cases, one is obligated to classify these stands as *Abies grandis-Pachistima* habitat types, since the redcedar is not reproducing itself. The stands listed in Table 2 represent a mixture of interactions between redcedar and grand fir; redcedar is reproducing itself well in all cases, but grand fir shows continuous reproduction in only a few, moderate regeneration in several others, and no reproduction in one of the stands. All of these stands would likely be classified as either *Thuja-Pachistima* habitat types or *Thuja-Athyrium* habitat types.

The fundamental basis for the Daubenmires' classification system is founded on their belief that within a given habitat, one tree species is competitively superior to all others, and an analysis of population structure will provide evidence of the tree species that will achieve monospecific dominance. However, even the Daubenmires (1968, p. 29, p. 55) recognize that this line of reasoning does not fit redcedar and grand fir interrelationships in Idaho. They state that grand fir is but "slightly less successful" than redcedar, and is usually not eliminated between destructive wildfires in the redcedar habitat types. The Daubenmires also describe the role of grand fir as "almost climax" in these habitat types.

TABLE 4. Cover class values for a group of common understory species found in the stands listed in Tables 1 and 2. Cover classes defined in text. + = present in stand, but not in plot.

Species	Lower Drainage Stands								Upper Drainage Stands					
	6	11	14	19	56	20	17	180	51	23	24	50	57	121
Shrubs:														
Amelanchier alnifolia	T		T	1	T	T	T	T	T	T		T	+	
Lonicera ciliosa	T				T	1	T							
Lonicera utahensis	T			1	T	T	T	T		T		T	2	T
Rhamnus purshiana	T	T		T	T	T	T		T	+	1	T	+	
Menziesia ferruginea				2				T	T		T	T	T	+
Spiraea betulifolia				1	T	1	T							
Rosa gymnocarpa	1	T	T	3	T	2	T	T	T	+	T	T		
Taxus brevifolia			+					3	2	2	3	1	2	2
Vaccinium globulare			1	2	T	1	T	T	2	1		1	+	3
Linnaea borealis			3	5	2	5	T	2	3	1		2	1	
Ferns:														
Adiantum pedatum	T	4	+		T		2			2	1			
Athyrium filix-femina		4	T	+					T	1	3		T	+
Gymnocarpium dryopteris		T	T						+	4	3		T	
Forbs:														
Adenocaulon bicolor	2	1	3	1	1	3	2	T	T	2	2		+	T
Asarum caudatum	2	2			+	1	3	1		3	3	T	T	+
Chimaphila umbellata				T	T	T		T	3			2	1	2
Clintonia uniflora	2	T	2	3	3	4	1	2	3	1	1	2	2	1
Coptis occidentalis	4	1	4	4	3	4	4	4	3	2	3	3	3	3
Cornus canadensis	T	T	1	2		2	2	2	1	1	T	1	2	
Circaea alpina		5				1	3			2	4			
Galium triflorum	1	2	1	2	1	2	1	T		2	1	T	2	
Goodyera oblongifolia	+		T	T	T	2	T	T		+	T	T	T	T
Osmorhiza chilensis	1	T	T	1	T	1	1		T	1	T	T	T	+
Pyrola asarifolia			T					T	1	+			T	1
Smilacina stellata	T		1	2	1	2	1	2		3	2	1	1	
Tiarella trifoliata	1	2	2	3	1	3	2		1	2	T	T	T	+
Trillium ovatum	T	+	T	1		2	1	T	1	1	2	T	T	T
Xerophyllum tenax									1			T	T	+

Observations and field data collected in the Selway-Bitterroot Wilderness support the view that a gradational shift exists between grand fir-dominated forests on better drained slopes to redcedar-dominated communities on moist streamside sites. Communities exhibiting shared dominance also exist. It is probably only to serve utilitarian purposes (forest management) that it would be justified to classify these cedar-grand fir forests arbitrarily into discrete habitat types, and avoid any effort to establish a separation based on natural discontinuities that do not appear to exist.

Discussion

The ecological behavior of *Thuja plicata* appears to be altered in some portions of the Selway-Bitterroot Wilderness, based on the data presented. Of major significance is the evident reduction or loss of reproductive redcedar capacity at lower elevations on the Selway River drainage system. The old-growth cedar stands at elevations below 1000 m have not successfully established reproduction for many years, and even trees up to 1 dm dbh are very rare. In these same lower drainage stands, *Abies grandis* is doing very well.

The reverse appears true for redcedar at higher elevations. Observations in upper drainage stands, above 1000 m, indicate a relatively healthy situation for redcedar. In many cases the redcedar reproductive layer is so dense that foot travel is difficult. Close examination of this cedar reproduction reveals that much of it has originated from vegetation propagation, and not sexual reproduction. This finding is identical to observations made on cedar regeneration in old-growth stands further north in Idaho, as well as in Glacier Park in northwestern Montana (Habeck, 1958). Seedlings originating from seed do not appear highly tolerant to dense shade.

It might be speculated that redcedar is not establishing itself well at lower elevations because conditions for vegetative reproduction are absent or limiting. Cedar limbs torn from trees by windstorm or snow are capable of producing adventitious roots if a moist microsite is available and remains moist during the summer. A majority of the cedar saplings examined at higher sites originate, however, from intact, lower limbs that touch the soil surface, or from small trees that are tipped over by heavy snowpacks.

If snow accumulations are higher and longer lasting at upper elevations and not so at lower sites, this difference might explain the situation discussed in this paper. To explain the data in Table 1 on this basis, one has to suggest that recent climatic modifications have taken place, leading to recent reductions in snowpacks. There is no evidence that this event has happened, however. Lower drainage positions seem to receive sufficient snow and total annual moisture to support cedar growth. Trail right-of-ways through the lower cedar groves, where sunlight penetrates to the ground layers, do support sexual seedling reproduction in small amounts.

There is another possible explanation for the lack of cedar reproduction at lower elevations; it includes a combination of events involving historical wildfire and past elk and deer populations in the Selway River drainage. Large fires occurring between 1910 and the mid-1930s created thousands of acres of seral brushfields (Giles and Snyder, 1971; Young and Robinette, 1939). The abundance of food and the remoteness of the area fostered the development of unusually high elk and deer populations. If the lower elevation cedar communities functioned to any degree as winter range,

a great pressure could have been exerted on any available winter food. It is possible that the small-sized cedars in the lower groves were simply destroyed by wintering elk and deer. Such a loss would have curtailed the most effective means the cedar has to reproduce itself in old-growth stands. Thus a major gap could have been created in the population structure of these lower groves, and the impact still remains today.

Within the Selway-Bitterroot Wilderness, *Thuja plicata* is responding to a deterioration of the Pacific maritime influence, and this response is likely the major reason it reaches its range limits in this region. If one believed that the range of redcedar was actually shrinking northward and westward, it would be expected that such a range reduction would first appear among the lower elevation populations; one could perhaps document that the cedar was not reproducing well on marginal sites (low elevations), but was continuing to do well where moisture was higher (upper elevations). The destructive influence of high numbers of elk and deer could then be interpreted as simply speeding up an inevitable reduction of the redcedar populations at lower sites.

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Literature Cited

Daubenmire, R. F. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. 9: 325-393.
———. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monog. 22: 301-330.
———. 1969. Ecologic plant geography of the Pacific Northwest. Madrono 20(3): 111-128.
———, and J. B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Wash. Ag. Exp. Sta., Tech. Bull. No. 60, 104 pp.
Finklin, A. I. 1974. Climate of the Selway-Bitterroot Wilderness. Office Report, Northern Forest Fire Lab., USDA Forest Service, Missoula. 28 pp.
Giles, R. H., and N. Snyder. 1971. Simulation Techniques in Wildlife Habitat Management. Unpub. Report, Region 1, USDA Forest Service. 20 pp.
Greenwood, W. R., and D. A. Morrison. 1973. Reconnaissance Geology of the Selway-Bitterroot Wilderness Area. Idaho Bureau of Mines and Geology, Moscow, Idaho. Pamphlet No. 154. 30 pp.
Habeck, J. R. 1968. Forest succession in the Glacier Park cedar-hemlock forests. Ecology 49: 872-880.
———. 1972. Fire Ecology Investigations in the Selway-Bitterroot Wilderness. USDA Forest Service, Region 1, Publ. No. R1-72-001. 119 pp.
———. 1976. Forests, fuels and fire in the Selway-Bitterroot Wilderness, Idaho. Proc. Tall Timbers Fire Ecology Conference. Vol. No. 14: 305-353.
Hitchcock, C. L., and A. Cronquest. 1973. Flora of the Pacific Northwest. Univ. Wash. Press, Seattle. 730 pp.
Leiberg, J. B. 1900. The Bitterroot forest reserve. Dept. of Interior, U.S. Gtol. Sur., 20th Annual Report. Part V: Forest Reserves, pp. 317-410.
Lindgren, W. 1904. A geological Reconnaissance across the Bitterroot Range and Clearwater Mountains in Montana and Idaho. Dept. of Interior, U.S. Geol. Sur., Prof. Paper No. 27. 123 pp.
Little, E. L. 1971. Atlas of United States Trees. Vol. 1 Conifers and Important Hardwoods. USDA Forest Service, Misc. Publ. No. 1146, 204 pp.
Steele, R., S. F. Arno, and R. D. Pfister. 1976. Preliminary Forest Hatbitat Types of the Nez Perce National Forest. USDA Forest Service, Inter. Forest and Range Exp. Sta. 71 pp.
Young, R. H., and W. L. Robinette. 1939. A Study of the Range Habits of Elk on the Selway Game Preserve. Univ. Idaho Bull., Vol. 45, No. 16. 47 pp.

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Grizzly Bears in the Southern Selkirk Mountains

Abstract

Records of grizzly bear sightings, incidents, and kills within the Selkirk Mountains of northern Idaho, northeastern Washington, and adjacent British Columbia provide evidence that the bear has been a resident in the area from historic time to date and that a small remnant population of grizzly bears is extant. Seventy sight records, or incidents, and 38 reported kills since the turn of the century have been mapped to determine the general range and habitat for the grizzly bear in this geographic area. Anomalies exist concerning previous reporting and apparent knowledge regarding this bear population: it has at different times been reported extirpated, transient, or simply overlooked. There exists confusion and lack of knowledge on the status and management of this grizzly population in the U.S. Habitat alteration through road construction, logging, and transmission line building in the southern Selkirk Mountains has been accelerating in recent years, and a critical need for additional studies on the grizzly bear and its habitat in this area is evident.

Introduction

The purpose of this paper is to provide record of the occurrence of grizzly bear (*Ursus arctos* Linné) for the Selkirk Mountains of northern Idaho, northeastern Washington, and adjacent British Columbia. Recent reports for the Purcell and Cabinet Mountains of northern Idaho are also given.

Historical accounts, records of kills, and frequency of recent observations from the area provide evidence that grizzly bears have been present from historic time to date and that a small but viable population is extant.

Methods

Little information had been recorded for the grizzly bear in the southern Selkirk Mountains and that which existed was scattered and fragmentary. In order to bring the information together for this paper, the literature and Fish and Game Department's records were reviewed, and personal communication and interviews were carried out with biologists, U.S. Forest Service personnel, and knowledgeable residents. Unpublished sources such as diaries and U.S. Forest Service file reports were also consulted. Only the accounts and records which the author considered to be reliable have been given.

The following zoological museums were contacted for possible records: Conner Museum, Pullman; Provincial Museum of Natural History, Victoria, B.C.; Thomas Burke Memorial Museum, Seattle; Universities of Idaho, Montana, and Puget Sound at Moscow, Missoula, and Tacoma, respectively. In addition, the files of E. Raymond Hall (pers. comm., 1976), which contain listings of grizzly specimens from major zoological museums such as the American National, Alberta at Edmonton, Berkeley, Carnegie, the Canadian at Ottawa, Chicago Field, and the U.S. National were consulted.

Results

Seventy sight records or incidents and 38 kill reports for the southern Selkirks (south of the Kootenay Arm) since the turn of the century are summarized in Table 1. Ten of the kill reports are for Idaho, 11 for Washington, and 17 for British Columbia since 1955. No museum records were found.

Locations of the accounts have been plotted in Figure 1 to establish the general range and distribution of grizzly bears for the area. Reported kill records for the entire West Kootenay British Columbia Fish and Wildlife Management unit are shown in Figure 2. General locations of two possible denning sites are reported in Table 1. Other important habitat features such as refuges for sow and cubs and spring food sources (Hamer, 1974) might be hypothesized from Table 1 and Figure 1, when the information is related to knowledge of the local area. Such application could be useful for management planning.

Although this paper is concerned primarily with the southern Selkirk Mountains, reports of grizzly bears from elsewhere in northern Idaho and adjacent northwestern Montana were received. These are summarized briefly herewith: in the Cabinet Mountains of Idaho, grizzly bears were reported from Trestle Creek, the Rattle Creek cabin, Bee Top, and Lightning Creek in the 1960s (E. Kulhanek, pers. comm., 1975). One grizzly reportedly was killed on Rapid Lightning Creek in 1953 (W. Peterson, pers. comm., 1975). At least three grizzlies were killed at a trail camp near Wanless Lake in the Cabinet Mountains in Montana in 1965. This story was communicated to the author by several different individuals at different times.

In the Purcell Mountains of Idaho, grizzlies have been reported from Canuck Creek and the head of Deer Creek near Canuck Pass; Harvey Creek in Sec. 8 and 17, T65N, R2E; and the Little Moyie River in adjacent British Columbia (P. Flinn, pers. comm., 1975). Other reports received were from Northwest Peak on the Montana-Idaho border.

Discussion

The area that the grizzlies have occupied since the turn of the century is dominated by the rugged Selkirk Mountains, until recent years a virtual wilderness visited only by occasional trappers, prospectors, woods workers, or U.S. Forest Service employees. Lack of knowledge on the status of this grizzly bear population is exemplified by Taylor and Shaw (1929), Rust (1946), and Dalquest (1948). These writers reported the area as included within the former range of the grizzly bear, but all expressed the opinion that the bear was largely extirpated from its range in northeastern Washington and Northern Idaho. Merriam (1922), on the other hand, stated (Fig. 3) that Idaho was one of the last "strongholds" of the grizzly and said that ". . . they are still fairly plentiful in the Priest Lake . . . forests . . . ."

Other confusing reports appear in the literature. Both Hayes and Hayes (1966) and Schoonmaker (1968) published correspondence from the Idaho State Fish and Game Department which fails to mention the occurrence of grizzly bears in the Selkirk Mountains of Idaho. In the same papers, however, the Washington State Game Department reported 8 to 10 grizzly bears for northeastern Washington. Since the Selkirk Mountains are interconnected between Idaho and Washington, both states would share the bears. Other such anomalies exist regarding the reporting and recording of

TABLE 1. Chronological listing of grizzly bear records for northeastern Washington (WA), northern Idaho (ID), and adjacent British Columbia (BC) from 1826-1977.

Date	Observer	Source	Account	State	Location (s)	Comments
1826-52		Douglas papers	Grizzly pelts traded		Upper Columbia, Kootenay, and Clark Fork Watersheds	Records from Fort Colville over a 27-year period show 2,653 grizzly bear pelts traded. The records indicate bear trade in the area picked up concurrent with decline in beaver returns (Johnson and Chance, 1974). The last 10 years record an average of 313 grizzly bear pelts a year being traded.
1853	Adams	Wright (1909)	Several kills	WA	"Somewhere in eastern Washington" and "North of the big bend of the Columbia River"	Original source—the adventures of James Capen Adams, mountaineer and grizzly bear hunter of California by T. H. Hittell, 1860.
Late 1800s	Wright	Wright (1909)	Kills and sightings	WA, ID, & BC	Spokane vicinity; Bitterroot Mountains; Selkirk Mountains, BC	Locations of Wright's accounts are difficult to determine. Wright remarks that in the spring of 1883, he was repeatedly informed "that in the hills surrounding Spokane there were plenty of grizzlies." Describing his first bear hunt on a weekend from Spokane, Wright says, "he and his friend broke every known rule of hunting with their lack of caution, carelessness in making noise and inexperience," ". . . and it spoke volumes for the number of these animals . . . roaming the hills, that we actually . . . saw 11." On Wright's first spring trip to the Selkirk Mountains of BC, he reported seeing 21 grizzly bears.
1889	Lindsley	Lindsley (1889)	10 kills	WA	Twenty miles up Pend Oreille River from the mouth.	Lindsley and his partner differentiated between "silvertips" and the black and brown bear they killed during one winter's hunt in the area.
c. 1903	Klockman & Houston	Klockmann Diary	Kill—sow with three cubs	ID	Near the Continental Mine	Klockmann states that they met grizzly bear on their "tramps." On this occasion they were forced to kill a sow with three cubs. The cubs were captured and kept for a number of years in Spokane's Twickenham Park in a pit cage specially constructed for them.

1913	Prouty	Layser (1972)	Kill	WA	Gypsy Meadows on Sullivan Creek	Bear killed by miners at the "meadows."
1918-19	Reid & Pagter	Huff (1940)	Tracks, sightings and one kill.	WA	Kettle Mountain Range (T. 36 N., R. 35 E.)	This is the only account of grizzly bear known by the author for the Kettle Mountain Range. Tracks and sightings over a 2-year period and a grizzly reportedly killed by a rancher.
1920s	Pauley	Layser (1972)	Numerous sightings and incidents; one kill	WA, & ID	Gold Creek, Cascade Creek, Salmo River, Hughes Meadows, Salmo Cabin	Pauley was an early Forest Ranger at Sullivan Lake during which time some of the first trails were opened up into the backcountry. He related one incident in which he and his son were on horseback and chased by a grizzly. A bear was shot at the Salmo Cabin that he estimated weighed near 800 pounds.
1921	Sutliff, Meyer, & Billings	Sutliff (1933)	Killed two and wounded another	ID	Hughes Meadows	The description in this article of grizzlies coming out into Hughes Meadows to feed may be an indication of the relative abundance of the bear at this time. Three grizzly bears were shot at the Meadows in 3 days in May 1921.
1922		Merriam (1922)		ID	Priest Lake area and Pend Oreille National Forest	Idaho is reported as, ". . . one of the last great strongholds of the grizzly; . . . they are still fairly plentiful in the Priest Lake . . . area." (See Fig. 3.)
1925	Stover	*Priest River Times* (6 Nov. 1975)	Kill	ID	Upper Priest Lake	Account published in 1925 and again in 1975. The pelt was sent to Spokane for tanning and mounting.
1930s	Monroe	Layser (1972)	Sightings	ID	Big Snowytop Mountain	Trappers frequently reported seeing grizzly on Big Snowytop Mountain.
1930s	Gudbaur	P. Flinn (pers. comm.)	Kill	ID	Parker Creek	The pelt was sent to the Idaho Fish and Game at Boise.
1930s	Luhr	Layser (1972)	Sightings	WA	Three Mile Creek	Bear was on dead cow near Luhr's homestead.
1930s	Cook	R. Cook (pers. comm.)	Incident	ID	Hughes Meadows	Bear thought to be a grizzly would break into the Forest Service cabin at Hughes Meadows every winter.

1936	White	L. White (pers. comm.)	Sightings	ID	Just above Hughes Meadows	Bear observed from about 75 yards.
1938	Luhr	Layser (1972)	Kill	WA	Hall Mountain	Grizzly was killed on the lake side of the mountain.
1938	Robins	R. Johnson (pers. comm.)	Kill	WA	Pend Oreille Co.	Pelt of a grizzly cub killed by L. Meck of Ione on Oct. 10—tagged by E. J. Robins at the Northern Fur Co., Spokane.
1939	Brash	D. Johnson (pers. comm.)	Kill	WA	Watch Creek—Salmo vicinity	Pelt at the Brash residence in Spangle, Washington.
1940s	Beaubier	Layser (1972)	Incident	WA	Salmo Cabin	Grizzly tore front of cabin off.
1940s	Beaubier & Sands	Layser (1972)	Sightings	ID	Little Snowytop Mountain	Forest Service lookout held in siege by a grizzly bear.
1940s	Nelson	Layser (1972)	Sightings	ID	Big Snowtop Mountain	Very large grizzly bear observed by a trapper who remembers the incident in particular because of the size of the bear.
1947	Peterson	W. Peterson (pers. comm.)	Sightings	ID	On the trail between Trapper Creek and Green Bonnet Mountain	Bear reportedly had very distinctive grizzly features in face, front shoulders, and hair.
1948	Brash	Scheffer (1950)	Kill	WA	Watch Creek—Salmo vicinity	Pelt or trophy at Brash residence in Spangle, Washington.
1949	Peterson	W. Peterson (pers. comm.)	Tracks	ID	Harrison Lake—head of Pack River	Tracks were in soft mud. Pad was 7½″ wide with prominent claw marks.
1950s	Wetterstrom	Layser (1972)	Sightings and tracks	WA, & ID	Little Snowytop Mountain, Watch Creek, Crutch Creek, Salmo River Trail, FS Trail 506 and 530	A number of sightings and tracks observed over a several-year period.
1952	Brash	Layser (1972)	Kill	WA	Head of Watch Creek	Bear reportedly was very large.

c. 1953	Stevens	P. Flinn & W. Peterson (pers. comm.)	Kill	ID	Rapid Lightning Creek, SW ¼ NE ¼ sec. 16, T. 58 N., R. 1 E.	Bear killed in sheep pen. Idaho Fish and Game personnel measured the bear to be 650 lbs., span between eyes 13 inches, top of head to nose tip 16 inches, green hide dimension 7 feet by 5 feet. Article on the bear published in the *Bonners Ferry Herald.*
1954	Washington State Fish & Game	McCracken (1957)	Kills	WA	" . . . neighborhood of the Idaho boundary in the northeastern corner of Washington . . ."	Correspondence from Washington State Game Department dated 3 June 1954 stated, "There have been several grizzly bears killed in the state in the past three or four seasons . . . I think that one group of hunters from the Spokane area killed two grizzly bears during the past hunting season."
1956	Lynch	Layser (1972)	Kill	ID	East of Kaniksu Mountain	Bear was causing problems around logging camp.
1956	Flinn	Layser (1972)	Sightings	BC	Meadows at Boundary Lake	Very large bear repeatedly seen.
Late 1950s	Gretchell & Luhr	Layser (1972)	Sightings	WA	Near Crescent Lake	Meadows at the old "Red Rooster" Lodge
1961	Bates	Layser (1972)	Sighting	BC	Near Nelway	
1962	Roskelly	Layser (1972)	Sighting	WA	South Fork Salmo River	Sow and cub. Roskelly had an article on the sighting in a Spokane newspaper.
Early 1960s	Evens & Luhr	Layser (1972)	Kill	WA	Meadows—SW ¼ sec. 10, T. 40 N., R. 43 E.	Bear would come out into the meadows in the spring and eat grass and hunt ground squirrels until someone shot it.
1960s		P. Flinn (pers. comm.)	Sightings	ID	Grass Mountain	
1966	Ferguson	D. Johnson (pers. comm.)	Sighting	ID	Forks of Granite Creek	
1966	Bierman	Layser (1972)	Sighting	ID	Hughes Ridge	

1967	Bohren	G. Gardner (pers. comm.)	Sighting	WA	South Fork Salmo River, sec. 4, T. 40 N., R. 45 E.	USGS survey crew saw sow and two cubs.
1967		J. Keniston (pers. comm.)	Sighting	ID	Marsh Lake near Saddle Mountain	
Late 1960s	Brineley	Layser (1972)	Sightings	BC	Salmo-Creston Highway	Maintenance workers on the highway often reported seeing grizzly bear cross the road.
1968	Montgomery	Montgomery (pers. comm.)	Probable tracks	ID	Upper Priest River trail	May in the snow.
1969	Gibney	Layser (1972)	Tracks	WA	Highline road at head of Totem Gulch	Hind print measured over 1 foot in length.
c. 1969	Gray	D. Gray (pers. comm.)	Sighting	BC	Corn Creek	Two young grizzlies in with cattle at Corn Creek.
1969	Bates	Layser (1972)	Tracks	WA	Gypsy Ridge and head of North Fork Sullivan Creek	
1970	Almen, Labrier & Hodgeboom	Layser (1972)	Tracks	WA	South Fork Salmo River	Pictures of tracks on file at Sullivan Lake Ranger Station.
c. 1970	Bandy	R. Bandy (pers. comm.)	Tracks	ID	Hughes Meadows	Tracks observed over a period of years up to about 1970 when cattle were taken into the Hughes Meadow allotment in spring. In 1970 the cabin was broken into by a grizzly.
1971	Gray	Layser (1972)	Tracks	BC	Head of Monk Creek on Ripple Mountain	Bear had just come out of den in late March. Tracks were observed from helicopter. Ripple Mountain thought to provide a denning area.
Early 1970s	Gray	D. Gray (pers. comm.)	Sightings	BC	Old campsite at Boundary Lake	Generally visited by a grizzly each fall on its way to hibernation.
1972-73	Rosgyn & Call	D. Call (pers. comm.)	Tracks	ID	West Fork Smith Creek, Sec. 28, T. 64 N., R. 3 W.	Tracks observed 2 years in a row going up West Fork Smith Creek trail when snow course was measured by Forest Service in May. A denning area is rumored to exist in the upper reaches of the West Fork Smith Creek.

1972	Stockman & Lee	D. Johnson (pers. comm.)	Sighting	ID	3½ miles up Cow Creek	Sow and two cubs in June.
1972	Gallis	D. Johnson (pers. comm.)	Sighting	ID	½ mile up Beaver Creek	Sow and two cubs in July.
1972	Loggers	D. Freddy (pers. comm.)	Tracks	ID	Rock Creek—Lime Creek. Sec. 2, T. 64 N., R. 5 W. and Sec. 35, T. 65 N., R. 5 W.	
1972	Freddy & Scamahorn	D. Freddy (pers. comm.)	Sighting	WA	Helmer-Mankato Mountains	Grizzly bear in open parkland, reared up on hind legs when airplane went over it.
1972	Kenny	D. Freddy (pers. comm.)	Probable sighting	WA	Hall Mountain	Bear in parkland; reared up on hind legs when airplane passed over it.
1972	Freddy	D. Freddy (pers. comm.)	Sighting	BC	Carolina Creek	Bear encountered in a clearcut.
1972	Freddy	D. Freddy (pers. comm.)	Tracks	BC	Next Creek	
1972	Lynch	D. Johnson (pers. comm.)	Sighting	ID	Canuck Basin (Purcells)	Sow and two cubs in August.
1972	USFS Employees	D. Freddy & R. Rogers (pers. comm.)	Sightings	ID	Cow Creek, just above Beaver Creek	Sow and two cubs rummaging through old Trapper Peak fire dump. Seen by USFS personnel more than once at close range.
1972		Anonymous	Kills	ID	Continental Mine and Trapper Peak near Trap Lake	Two possible illegal grizzly kills.
1972	USFS Engineer	J. Keniston (pers. comm.)	Sighting	ID	Blue Joe Creek, Sec. 28	
1972	Gallis	D. Johnson (pers. comm.)	Tracks	ID	Head of Smith Creek	

1972-73	BC Guide & Outfitter	R Demarchi (pers. comm.)	Several sightings	BC	Both east and west of Salmo River	
1973	Ellis	C. Ellis (pers. comm.)	Sighting	ID	Phoebe Tip	Young grizzly photographed in old Trapper Peak burn. Author has copies of photograph.
1955-73	BC Fish & Game	K. Lloyd (1975)	16 kills	BC	Adjacent BC south of the Kootenai arm	Reported kills from the BC Fish and Game Files from 1955-73.
1974	Stark	J. Keniston (pers. comm.)	Sighting	ID	Upper Priest, sec. 15, T. 64 N., R. 5 W.	Sow and two cubs.
1974	Gallis	D. Johnson (pers. comm.)	Tracks	ID	Shorty Peak Trail	
1974	Schroeder & Todd	D. Johnson (pers. comm.)	Sighting	BC	One mile up Monk Creek	Large grizzly track left from hind foot measured 9" x 14".
c. 1974	Stockman	D. Call (pers. comm.)	Sighting	ID	Grass Creek, tributary to Boundary Creek	Sow and two cubs.
1974	Benwah	J. Keniston (pers. comm.)	Sighting	WA	South Fork Salmo River—Section 5	
1974?	Smart	J. Keniston (pers. comm.)	Sighting	ID	East of unnamed lake on west side of Big Snowytop Mountain	
1974	Durham	J. Keniston (pers. comm.)	Tracks	ID	FS Trail 530 in section 17, west of Big Snowytop Mountain	Pictures taken of tracks.
1974	Johnson & Money	D. Johnson (pers. comm.)	Tracks	BC	East side of Stagleap Provincial Park	
1975	Lyons	J. Keniston (pers. comm.)	Tracks	ID	Near FS Trail 311 just west of Hughes Meadows	Pictures taken of tracks.

1975	Hunters	D. Gray (pers. comm.)	Kill	BC	Corn Creek	Adult male killed by hunters who reported they were "attacked." BC Fish and Game at Creston has pelt.
1975	Gray	D. Gray (pers. comm.)	Live trapped and tranquillized	BC	5 miles west and 1 mile south of Creston	Bear was on a dead cow and would not leave. (D. Gray, Creston, BC., has pictures of the bear.)
1975		J. Keniston (pers. comm.)	Tracks	WA	South Fork Salmo River	Confirmed grizzly tracks—5 May.
1975	Bennett	P. Flinn (pers. comm.)	Sighting	ID	Lost Creek	Sow with two large cubs. The sow attacked the tree skidder being operated by loggers.
1967-75	Various sources	U.S. Forest Service 1975	Sightings and habitat mapped	ID	Upper Smith Creek, Upper Cow Creek, and Upper Grass Creek	Statement excerpt, ". . . grizzlies have been regularly observed . . . since 1967 . . . a large number of sightings have been reported . . ." from the locations cited.
1976	Miller, D.	D. Johnson (pers. comm.)	Tracks	BC	South side Carolina Creek	Late May.
1976	Cable, R.	Creston, B.C. Fish and Wildlife Report No. 112	Attack	BC	Near Boundary Lake	Member of survey crew working on the proposed 500KV line attacked by grizzly on July 10. Report filed by R. J. Hoar, BC Fish and Wildlife. Also comments that a large boar grizzly had been sighted in the same area earlier that spring.
1977	Smith, G.	D. Johnson (pers. comm.)	Sighting	WA	Soldier Creek, Sec. 29, T 60 N., R 3 W.	Mr. Smith has seen and photographed grizzlies in Alaska and he is also familiar with black bear.

grizzly bear information from this area and have contributed to confusion regarding the status of this bear population in the United States. Recent articles on the status of the grizzly bear in the United States have overlooked or failed to mention this population.

Lauchart (1975) stated that grizzlies still occur in northeastern Washington, and estimated a population of 10 grizzly bears for the entire state. The U.S. Forest Service Smith Creek planning unit draft environmental statement (1975) provided a map of grizzly bear habitat for part of the Selkirk Mountains in northern Idaho and stated ". . . prior to the 1967 Trapper Peak fire only a few infrequent grizzly bear sightings were made. Since that time, grizzlies have been regularly observed . . . a large number of sightings have been in upper Smith, Cow and Grass Creeks." One of the possible reasons given for the increase in grizzly bear encounters is improved access created by roads constructed for the Trapper Peak fire and Smith Creek.

General evaluations of the grizzly bear population in the Selkirk Mountains of the United States traditionally have labeled the bears in northern Idaho and northeastern Washington as "wandering individuals" or "migrants from Canada." In view of the fact that tagged grizzlies elsewhere have been reported to travel up to 65 miles in the course of a summer and that pregnant females or males seeking new range may travel widely (Mundy, 1963), some of the bears observed in the United States may indeed range between Canada and the United States and between Idaho and Washington. This fact, however, should not serve to devalue the bear population; rather, it is an important consideration in the protection and management of the grizzly for this area. Cooperative management is being treated by the British Columbia Fish and Wildlife in their preparation of a "Kootenay Region grizzly bear management plan" (R. Demarchi, pers. comm., 1975).

Evidence presented in Table 1 indicates that northeastern Washington and northern Idaho possess habitat that has supported a grizzly population from historic time to date. These facts should be more than sufficient to establish the population as resident under interpretation of that term in the Endangered Species Act of 1973. The state of Idaho has protected the grizzly since 1947, although the law states that any bear may be taken if it molests livestock. The Washington State Game Commission closed all seasons on grizzlies in 1969. However, grizzly bears are still hunted legally in adjacent British Columbia.

Although grizzly habitat is often thought to include only open subalpine forest and parkland, many of the sight and kill records for grizzly bears in this area are from heavily timbered *Thuja plicata — Tsuga heterophylla* forest, or along streamsides and meadows in the *Thuja-Tsuga* zone, as well as in the subalpine areas. Mundy (1963) reported that in early spring, grizzly bears utilized heavily timbered areas and in June moved up into avalanche areas and alpine meadows. Habitat disturbance within the area of discussion has greatly increased in the past two decades and if continued as projected could seriously threaten this grizzly population. Access has been greatly increased in the area in recent years. Roads were constructed into the Rock Creek-Lime Creek area in northern Idaho in the late 1950s. The Salmo-Creston highway and power transmission line in adjacent British Columbia were built in the 1960s. So, too, the Trapper Peak fire and its access roads and the Smith Creek road construction occurred in the 1960s in northern Idaho. The new Salmo-Sullivan road in northeastern Washington, along with numerous logging roads and extensive logging in the United States

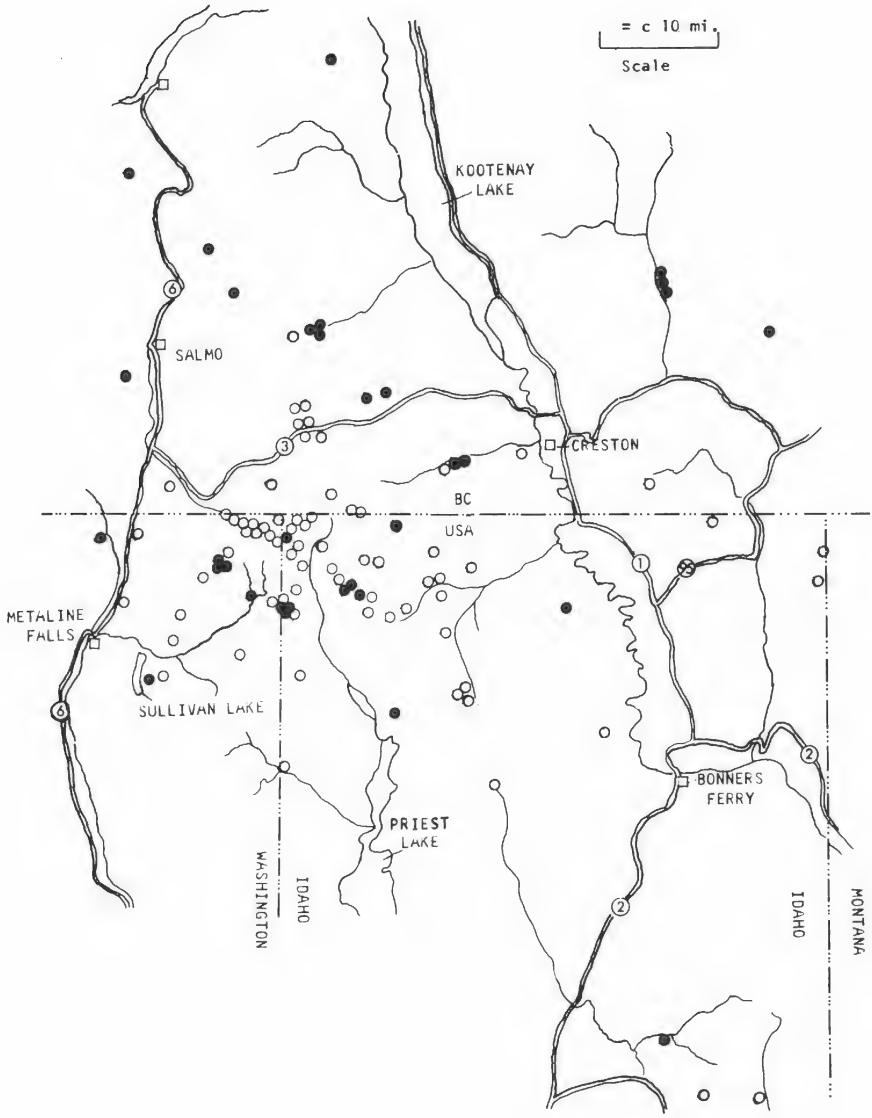

Figure 1. Approximate distribution of grizzly bear in southern Selkirk Mountains from 1900-76 based on records from Table 1. Information for other than the Selkirk Mountains is also shown.
● = kill
O = sighting or incident

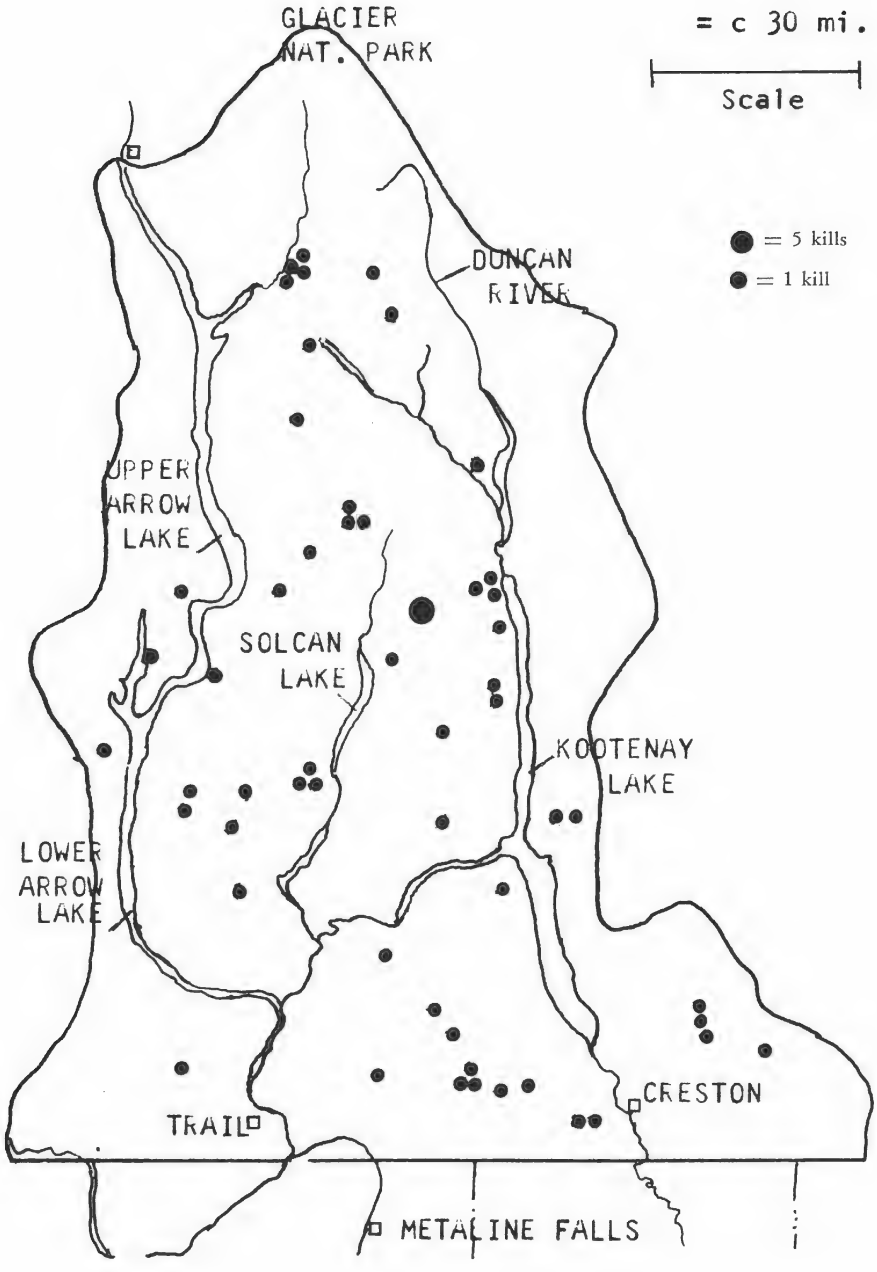

Figure 2. Map showing approximate locations of reported grizzly bear kills in the B.C. Fish and Wildlife West Kootenay management unit from 1955-75 (from Lloyd, 1975).

and British Columbia, also took place during the same decade. A 12-inch natural gas transmission line, a planned 500 kilovolt powerline, relocation of a part of the Salmo-Creston highway, talk of a 5-foot coal slurry pipe line are things in planning or progress within the bears' range in adjacent British Columbia. These activities threaten not only habitat but increase the man-grizzly encounters (Table 1); they increase the probability of grizzlies being destroyed as nuisance, and make the bears more vulnerable to hunters in general.

There exists a critical need for additional studies on the grizzly bear in the southern Selkirk Mountains to establish the bear's population status more clearly, and to define and assure protection of habitat.

Figure 3. Map of the distribution of grizzly bear by C. H. Merriam in 1922 (from *Outdoor Life*, Dec. 1922; reprinted with permission from The Popular Science Publishing Company).

No museum records of grizzly bear from the Selkirk Mountains within the United States were located, nor do the respective State Fish and Game Departments have pelts or skulls. Efforts should be made to acquire the gift of existing private collections to local museums for record and preservation.

Acknowledgments

The author wishes to express his thanks to the many individuals and agencies cited herein who by their contributions of information and assistance made this article possible. Appreciation is also expressed to Drs. Charles J. Jonkel and Donald R. Johnson for critical review of the manuscript, to E. Raymond Hall for review of his personal research files for possible museum records, and to the curators of the other museums listed.

Literature Cited

Dalquest, W. W. 1948. Mammals of Washington. Univ. Kansas Publ. Mus. Nat. Hist. 2. 444 pp.
Douglas, J. Papers, 1826-1862. Prov. Archives, Victoria, B.C.
Hamer, J. D. W. 1974. Distribution, Abundance and Management Implications of the Grizzly Bear and Mountain Caribou in the Mountain Creek Watershed of Glacier National Park, British Columbia. U. of Calgary, Alberta, M.Sc. thesis. 163 pp.
Hayes, B. D., and E. Hayes. 1966. The Grizzly Bear, Portraits from Life. University of Oklahoma Press, Norman. 386 pp.
Huff, R. 1940. History of grazing on the Colville National Forest. Unpubl. USDA Forest Service files, Colville, Wa.
Johnson, D. R., and D. H. Chance. 1974. Presettlement Overharvest of Upper Columbia River Beaver Populations. Can. J. Zool. 52(12): 1519-1521.
Klockmann, A. K. Diary, 1883-1940. Bonners Ferry Herald (in serial form) by P. M. Flinn, 1959.
Lauchart, J. B. 1975. Grizzly bear section. Big game status report, pp 219-226. Washington State Game Dept., Olympia.
Layser, E. F. 1972. Notes on grizzly bear sightings in northeastern Washington and adjacent northern Idaho. Murrelet 53: 8-9.
Lindsley, H. C. 1889. The Pend Oreille Country. Forest and Stream 33: 227-228.
Lloyd, K. A. 1975. Hunters, Harvest and Management of Grizzly Bear (*Ursus arctos* Linné) in the Kootenay Region of British Columbia. (Dept. of Zoology), Univ. of British Columbia, Vancouver, BS thesis. 92 pp.
McCracken, H. 1957. The Beast That Walks Like a Man. Oldbourne Press, London. p. 189.
Merriam, C. H. 1922. Distribution of grizzly bear in U.S. Outdoor Life (Dec.), pp. 405-406.
Mundy, K. R. D. 1963. Ecology of the grizzly bear (*Ursus arctos* L.) in Glacier National Park, British Columbia. Univ. of Alberta, Edmonton, M.S. thesis. 103 pp.
Rust, H. J. 1946. Mammals of northern Idaho. J. Mamma. 27(4): 308-325.
Scheffer, V. B. 1950. Grizzly bear killed in Washington. Murrelet 31: 15.
Schoonmaker, W. J. 1968. The World of the Grizzly Bear. J. B. Lippincott Co., New York. 180 pp.
Sutliff, C. B. 1933. Charging death; the true account of a grizzly hunt that almost ended fatally. Outdoor Life (Feb.), pp. 15-17, 48-50.
Taylor, W. P., and W. T. Shaw. 1929. Provisional List of Land Mammals of the State of Washington Mus. Occas. Pap. 2. 31 pp.
USDA Forest Service. 1975. Smith Creek Land Use Plan Environmental Statement. R1-76-2 (July). Kaniksu N.F., Sandpoint, Id., pp. 138-141.
Wright, W. H. 1909. The Grizzly Bear. Charles Scribner's and Sons, New York. 274 pp.

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Effects of Controlled Slash Burning on the Mountain Beaver (Aplodontia rufa rufa)

Abstract

A study was done on the effects of controlled slash burning on mountain beaver populations and movements. Results indicated that the fire, which removed most of the vegetation and left little, if any, slash accumulations remaining within the unit, substantially reduced the mountain beaver population level within the unit. The fire left a large unburned part within the unit (20 percent unburned): 80 percent of the estimated population survived; most of these animals were captured in the unburned part of the unit after the fire. The fire did not cause animals captured after the burn to move out of their home ranges, although an animal tended to move to an unburned area if the area were located within the animal's home range. Predator activity within the units increased after the fire, probably because of the presence of carcasses of animals which had been killed by the fire.

Introduction

The mountain beaver, *Aplodontia rufa,* is one of the most primitive rodents known. This animal's present distribution is limited to the Pacific Northwest, ranging from central California north to southern British Columbia. Ancestral aplodontids date back to the upper Eocene, with fossil evidence occurring in the Northwest as well as in several other western states and also in Asia (Shotwell, 1958). The mountain beaver's present restricted distribution is probably caused by physiological limitations (Johnson, 1971; Kinney, 1971).

Of the family Aplodontidae, only one genus and species, *Aplodontia rufa,* remains in existence today. This species includes seven subspecies within its range (Godin, 1964), *A. r. rufa* being the subspecies used in the present study. *Aplodontia,* which resembles a tailless muskrat, leads a semi-fossorial, chiefly nocturnal, herbivorous life in the moist Coast Rain Forest Biome. Godin (1964) has reviewed the literature on the mountain beaver, and several recent theses have been written on the food habits (Voth, 1968; Allen, 1969) and environmental physiology (Johnson, 1971; Kinney, 1971) of this animal.

Aplodontia is of little economic importance except as it occurs during reforestation on conifer plantations. On these plantations, damage by mountain beavers to conifers, particularly to Douglas-fir trees and seedlings, has often been shown to reduce significantly survival of these trees. King (1958), in a study concerning damage and survival of trees on a conifer plantation, concluded that mountain beaver damage was the greatest single cause of tree mortality on that plantation. Munger (1943) also showed that mountain beavers could be a principal cause of plantation failure. Recent surveys by Weyerhaeuser Company (pers. comm.) have indicated that up to 25 percent of a plantation can be damaged by mountain beavers. Recent economic analyses by this company have also

shown that this damage could produce a potential Net Present Value loss of several million dollars over the next two decades (Motobu *et al.,* 1975).

Several methods to control the damage caused by this rodent have been investigated (Seals, 1966; Martin, 1968; Oita, 1968). The present study involves the effects of controlled slash burning on mountain beaver populations and movements and its implications in terms of controlling regeneration damage by direct reduction of mountain beaver population levels as well as by providing better accessibility to the area for trapping and/or baiting crews and for predators. Tevis (1956) reported a reduction in population levels in forest mice as a result of slash burning, but no report has yet been published on the effects of slash burning on mountain beavers. Black and Hooven (pers. comm.), however, in preliminary studies in 1974, noted a decrease in mountain beaver populations as a result of slash burning.

Methods and Materials

Two study sites, A and B, were selected; they were located in Section 35 (Township 17 North, Range 7 West), approximately 40 km southwest of Montesano, Washington, in Grays Harbor County (elevation 180 m) (Fig. 1). These two sites were selected because they exhibited similar characteristics of size (7 and 9 ha, respectively), topography (both were draws, with similar slopes and aspects), vegetation, and amounts of residual slash accumulation. Both units also supported medium to heavy mountain beaver populations, and were bordered on at least one side by second growth conifer stands supporting light mountain beaver populations. Both units also had similar histories of logging, having been logged to remove the merchantable timber approximately one year prior to this study, and having had remaining vegetation cut down or slashed at about the same time to prepare the sites for burning.

Representative samples of the mountain beaver populations on both units were live-trapped, tagged, and released prior to the burn—33 animals on unit A, 31 animals on unit B during the period extending from June 26 to July 19, 1975. The traps used were welded-wire live traps, either 15 by 15 by 61 cm (double door model) or 15 by 15 by 48 cm (single door model). These were placed in main runway tunnels. Trapping was done on a three-night rotational basis, and trapping sites, each involving four to six live traps, were spaced 46 to 68 m apart in a well-distributed pattern over the units.

When an animal was captured, it was tagged in both ears, and weight, sex, and approximate age were recorded. If an animal showed signs of being weakened by overexposure in the trap, it was given an oral or rectal administration of 10 to 12 milliliters of a 50 percent dextrose/water solution using a plastic hypodermic syringe (without needle) (Dodge and Campbell, 1965), and kept under observation until it was sufficiently recovered to be released. All captured animals were subsequently released in the same runways in which they had been caught. Each of these release points was then marked with an iron reinforcing bar and its location mapped, to ensure its relocation after the fire. Any recaptures of tagged animals were also marked and mapped, and the distances each of these animals had moved from their first release points were recorded.

Prior to the fire, the resident mountain beaver population within a 60-m wide strip of the conifer border adjoining unit A was also removed (Fig. 1) to determine

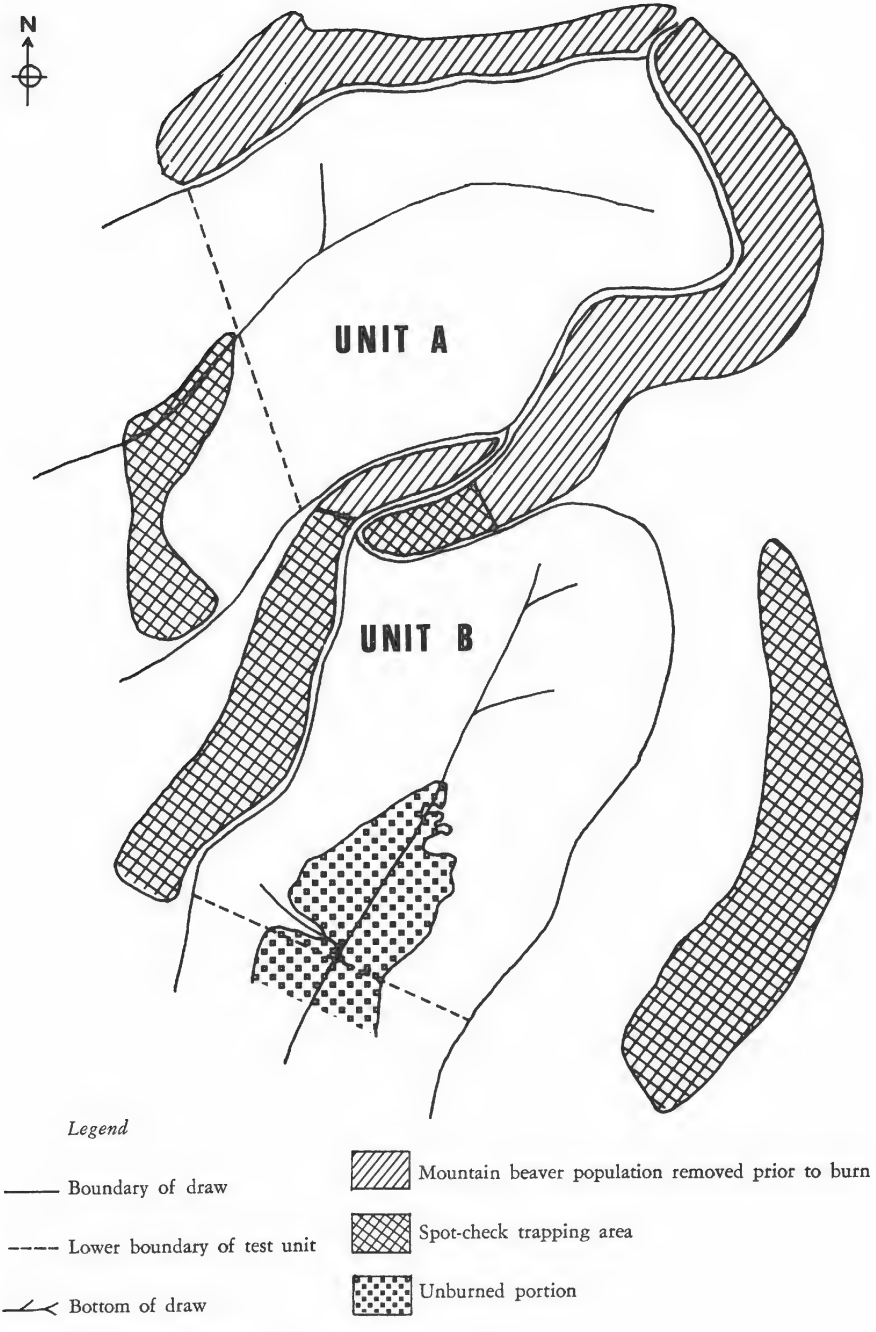

Figure 1. Map of units A and B after the burn.

if the lack of a population in the border would influence the movement of animals out of the burn area during or after the fire. Traps were also set in the border during the burning of the sites in order to catch possible emigrants.

Approximately 1.5 to 2 weeks before burning, the two units were spot-sprayed by helicopter with a dinitro desiccant to kill the vegetation and prepare the sites for burning. On August 11, 1975, the two units were burned by a controlled broadcast burn, using a helicopter ignition system.

After the fire, from August 26 to September 19, when sufficient sign of mountain beaver activity was observed, the two units were kill-trapped, using Number 110 Conibear traps, to capture as many of the individuals that had survived the burn as possible. Each animal was then weighed, and sex, approximate age, and any signs of burn injuries sustained from the fire were recorded. The distances from the original release sites that tagged animals had moved were also recorded The traps set in the border of unit A were checked periodically for possible emigrants moving out of the burn area.

To test further the possibility of tagged animals moving out of the burn areas, spot-check trapping was done in the peripheral areas surrounding units A and B not already set with traps (Fig. 1). These spot checks were set in areas of mountain beaver activity covering a 90- to 150-m wide strip around the units. The conifer border of unit B was also trapped to check for tagged animals.

Within the units, checks for evidence of animals having been killed by the fire were run periodically beginning two days after the fire. Periodic checks on predator activity within the burn areas were also done.

Results

The fire in unit A left very little residual slash accumulation within the unit. The fire in unit B, however, left approximately 1.8 ha of unburned brush and slash within the unit (20 percent of the unit); most of this unburned part was contained in the lower half of the draw.

Approximate estimates of the mountain beaver populations within each unit at the time of burning were obtained by adding the number of animals surviving the fire to the number of animals killed as a direct result of the fire (Table 1). In unit A, the approximate population estimate before the fire was 58 animals, and in B it was 66 animals. Thus, in unit A, 30 animals, or 51 percent of the estimated population present at the time of the burning, had been killed by the fire, whereas 29 animals, or 49 percent, had survived. One of the survivors was a tagged animal which was caught two days after the fire at the edge of the conifer border of A. In unit B, however, only 13 animals, 20 percent of the population, had died as a result of the fire, whereas 53 animals, or 80 percent, had survived. Of the survivors, 87 percent (46 animals) were captured in the unburned part of the unit.

In unit A, 11 tagged animals, representing 33 percent of the animals tagged in unit A previous to the fire, were recaptured after the burn; in unit B, 10 animals, or 32 percent of the tagged animals released on that unit prior to the fire, were recaptured after the burn. Of the tagged animals recaptured in B, four of the seven tagged animals originally released in the unburned area of B were recaptured after the

fire. Only 6 of 24 tagged animals originally released in the burned part of B were recaptured after the fire. Two of these had stayed within the burned area and four had moved from their original release sites into the unburned area.

TABLE 1. Effects of slash burning on mountain beaver populations.

	Unit			
	A	%	B	%
Total estimated population at time of fire	58		66	
Number of animals killed by fire	30	51	13	20
Number of animals surviving fire	29	49	53	80
Number of tagged animals recaptured after the fire (Percentage is of total tagged animals released on each unit)	11	33	10	32
Number of animals with signs of burn injuries (Percentage is of animals surviving the fire for each unit)	8	28	8	15

Eight individuals (28 percent) of the surviving animals in unit A showed signs of burn injuries as a result of the fire, but only 15 percent (8 animals) of the survivors in B showed evidence of burn injuries. Three out of the seven animals caught in the burned part of unit B exhibited burn injuries, but only five out of 46 of the animals caught in the unburned part of B gave any evidence of injury. There also appeared to be a slight reduction in the average weights of the animals which had survived the fire in A, whereas there was a slight gain in the weights of animals captured after the burn in B.

The fire did not appear to have any effect on age classes or sexes within either population. The proportions of the age classes within the populations after the fire, as well as the sex ratios observed, did not differ substantially from results obtained from Weyerhaeuser Company's animal damage control data (M. Jones, pers. comm.) concerning normal mountain beaver populations, nor did they differ from the results of studies done by Voth (1968) or Lovejoy (1972).

The fire also did not appear to affect the movements of the tagged animals recaptured after the fire (Table 2). There was no apparent difference in the average distances recaptured animals had moved before or after the fire in either unit. The average distances of movement recorded after the burn were also similar to the results of the normal home range and movement studies done by Martin (1971) and Lovejoy (1972).

Evidence did seem to indicate, however, that animals tended to move to an un-

TABLE 2. Movements of mountain beavers before and after slash burning. (Measurements in meters.)

	Unit	
	A	B
Average distance moved prior to fire	40 (14 to 90)	26 (12 to 52)
Average distance moved after fire	36 (2 to 91)	27 (2 to 63)

burned area if it occurred within their normal range of movement. Four of the surviving tagged animals in unit B moved from their original release sites, located in burned areas, to the unburned part of B after the fire. The average distance moved was 47 m (range: 21 to 63 m), still within the normal average and maximum movements recorded by Lovejoy (1972). The original release sites of the other two tagged animals remaining in the burned area of B after the burn were located 150 m or more away from the unburned part of B, distances which exceeded the normal range of movements calculated by Lovejoy (1972); these animals were not observed to move to the unburned area after the fire.

Evidence was insufficient to indicate the influence of fire on the animals' movements out of the burned areas. One tagged animal was caught on the edge of the border adjoining unit A, as mentioned previously; but the distance it had moved from its original release site still did not differ substantially from the normal average maximum distance reported by Lovejoy (1972). Six untagged animals were caught in the conifer border of A within one week after the fire, after which time only one more animal was caught until the time the border traps were removed, on September 23, 1975. Although these animals could very possibly have moved to the border from the burn area shortly after the burn, no definite conclusions could be drawn concerning their origins, because they were not tagged. No other tagged animals were recaptured in the border of B or in any of the spot-check trapping done around the edges of the units.

Predator activity within the units, particularly coyote *(Canis latrans),* increased markedly after the fire, as evidenced by paw prints and signs of digging to uncover mountain beaver burrows. No digging by coyotes had been observed in the units prior to the fire, although numerous paw prints had been noted. After the fire, however, signs of 22 digging sites to uncover mountain beaver burrows in unit A were observed, and 12 digging sites were found in unit B. All digging sites were found in burned areas. Of the diggings found in unit A, sixteen (73 percent) occurred within the first 2.5 weeks after the fire. In B, seven (58 percent) of the diggings occurred within the first three weeks after the fire. Most of the diggings were to recover carcasses of animals killed by the fire, as evidenced by the rotting or burned remains of beavers found near the digging sites. Some of the diggings, however, were attempts to capture live animals, as indicated by the extensiveness of the diggings. Other predators observed in the burned area were longtail weasels *(Mustela frenata)* and red-tailed hawks *(Buteo jamaicensis).* Ravens, crows, and turkey vultures were also seen on the sites after burning.

Discussion and Conclusions

In unit A, the estimated population level was reduced 51 percent by the fire. In unit B, which contained a large part of unburned area, the population level was reduced by only 20 percent; most of the survivors were captured in the unburned part of the unit. A proportionately greater number of tagged animals also survived in the unburned part of B. The proportion of animals sustaining injuries from the fire was also shown to be higher in A than in B. In addition, in unit B, a much smaller percentage of the animals found in the unburned part showed signs of burn injuries.

The fire had no apparent effect on the different age classes or sexes within the two populations.

The fire also did not cause the animals remaining in the units after the burn to move out of their normal home ranges, although indications were that animals would go to an unburned area within the burn if it occurred within their normal range of movement. Because only one tagged animal was recaptured within the borders of either unit, this animal still being within its normal range, it would seem that the animals present at the time of burning either stayed within the units during and after the burn, or moved out beyond the borders of the units and were not recovered. Evidence indicates that many of the tagged animals were probably killed by the fire, but this hypothesis could only be proved by more direct evidence, such as that obtained by radio tracking.

Predator activity in the burned areas also increased after the fire, particularly coyote activity. This increase was probably caused in part by the presence of carcasses within the burns, as well as by improved accessibility of predators to their prey.

The results of this study have direct managerial implications in forest regeneration and have been reviewed in a previous paper (Motobu *et al.,* 1975). Follow-up research work done by Weyerhaeuser Company personnel (pers. comm.) has also shown that the intensive removal trapping done after the fire has alleviated to a great extent the damage caused by mountain beavers to recently planted Douglas-fir seedlings within the units. Research is continuing on this subject.

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Literature Cited

Allen, L. O. 1969. Preferential Food Habits of *Aplodontia rufa.* Central Washington State College, unpublished Master's thesis. 55 pp.

Dodge, W. E., and D. L. Campbell. 1965. Two techniques to reduce capture mortality. J. Mammal. 40(4):707.

Godin, A. J. 1964. A Review of the Literature on the Mountain Beaver. U.S. Dept. of the Interior, Bureau of Sport Fisheries and Wildlife, Special Scientific Report, Wildlife No. 78. 52 pp.

Johnson, S. R. 1971. The Thermal Regulation, Microclimate, and Distribution of the Mountain Beaver, *Aplodontia rufa pacifica* Merriam. Oregon State University, unpublished Ph.D. thesis. 164 pp.

King, J. E. 1958. Development of a stand of coniferous reproduction and interplanted Douglas-fir. Northw. Sci. 32(1):1-8.

Kinney, J. 1971. Environmental Physiology of a Primitive Rodent. University of Oregon, unpublished Ph.D. thesis. 181 pp.

Lovejoy, B. P. 1972. The Capture-Recapture Analysis of a Mountain Beaver Population in Western Oregon. Oregon State University, unpublished Ph.D. thesis. 105 pp.

Martin, P. 1968. Development and Use of Toxic Foam to Control Mountain Beavers. Part I. Field evaluation of lethal agents by radio-tracking. Wildlife and Reforestation Symposium, School of Forestry, Oregon State University. 6 pp.

———. 1971. Movements and activities of the mountain beaver *(Aplodontia rufa)*. J. Mammal. 52(4):717-723.
Motobu, D. T., J. Todd, and M. Jones. 1975. Effects of Slash Burning on Mountain Beaver Populations and Movements. Weyerhaeuser Forestry Research Technical Report No. 40. 7 pp.
Munger, T. T. 1943. Vital statistics for some Douglas-fir plantations. J. Forestry 41:53-56.
Oita, K. 1968. Development and Use of Toxic Foam to Control Mountain Beavers. Part II. Toxic foam tracking compound. Wildlife and Reforestation Symposium, School of Forestry, Oregon State University. 7 pp.
Seals, S. J. 1966. Damage and Control of Mountain Beaver. U.S.F.S. Presented at N. W. Sec. of W. L. Soc. 8 pp.
Shotwell, J. A. 1958. Evolution and biogeography of the aplodontid and mylagaulid rodents. Evol. 12:451-484.
Tevis, L., Jr. 1956. Effect of a slash burn on forest mice. J. Wildl. Manage. 20(4):405-409.
Voth, E. H. 1968. Food Habits of the Pacific Mountain Beaver, *Aplodontia rufa pacifica* Merriam. Oregon State University, unpublished Ph.D. thesis. 263 pp.

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Invertebrate Density and Biomass Distribution Patterns in an Old-Field Community in South-Central Washington

Abstract

Invertebrate density and biomass were estimated in an old-field community vegetated primarily with cheatgrass (*Bromus tectorum* L.) in south-central Washington. An analysis in terms of taxonomic and trophic groupings revealed mites, beetles, and thrips to be the most abundant taxa present. Beetles and grasshoppers contributed most to total biomass. Maximum density and biomass values were obtained in April and May, respectively, the period of peak green plant standing crop values. Herbivores and omnivores were the largest trophic groups in terms of density and biomass.

Introduction

Cheatgrass (*Bromus tectorum* L.) is an introduced annual grass that readily invades disturbed habitats of south-central Washington. Once established, cheatgrass is able to maintain itself for long time periods. Cheatgrass communities on the Energy Research and Development Administration's Hanford Reservation have existed as a continuous sward for over 30 years, with little evidence that nearby native species are regaining dominance (Rickard, 1972).

Although cheatgrass communities are now an important component of the ecology of the grassland regions of this area, little is known about associated animal populations. This study was designed to ascertain the taxonomic and trophic distributions of invertebrate density and biomass in a cheatgrass community. An abandoned wheatfield last cultivated in 1943 served as the study site. Cheatgrass is the dominant plant species present, but others such as yellow salsify *(Tragopogon dubius),* lanceleaf microseris *(Microseris lacinata),* jagged chickweed *(Holosteum umbellatum),* and tumble-mustard *(Sisymbrium altissimum),* are common (Rogers and Uresk, 1974). The old-field is about 400 ha in size and is located at an elevation of 533 m.

Methods

Invertebrates were sampled at one-month intervals from April to August using a drop-trap technique. A cage 0.5 m^2 in area, 40 cm tall, and covered with 32 x 32 mesh saran netting was suspended from a tripod device on the day prior to collection. On the sample day the tripod was approached with care and the cage released from a distance

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of about 6 m using a trip cord. Large invertebrates (grasshoppers, flies, etc.) were removed by hand or with a small aspirator. The vegetation within the cage was clipped by reaching through an access hole protected by tubular stocking material. A 10 cm diameter hose connected to a D-Vac suction apparatus was then used to remove all material down to bare ground. Collected plant and invertebrate material was taken to the laboratory and the invertebrates were extricated into 75 percent ETOH using a Berlese funnel technique. Specimens were then sorted by hand, measured, and identified with the aid of a dissecting microscope. Weight estimates were calculated for individual specimens using length-weight regression equations developed by Rogers *et al.* (1977). Average weights were determined by drying and weighing representative specimens where regression equations were not available.

Results

The seasonal distribution of estimated density and biomass values are shown in Figure 1. The highest density values were obtained in April, although the actual peak density

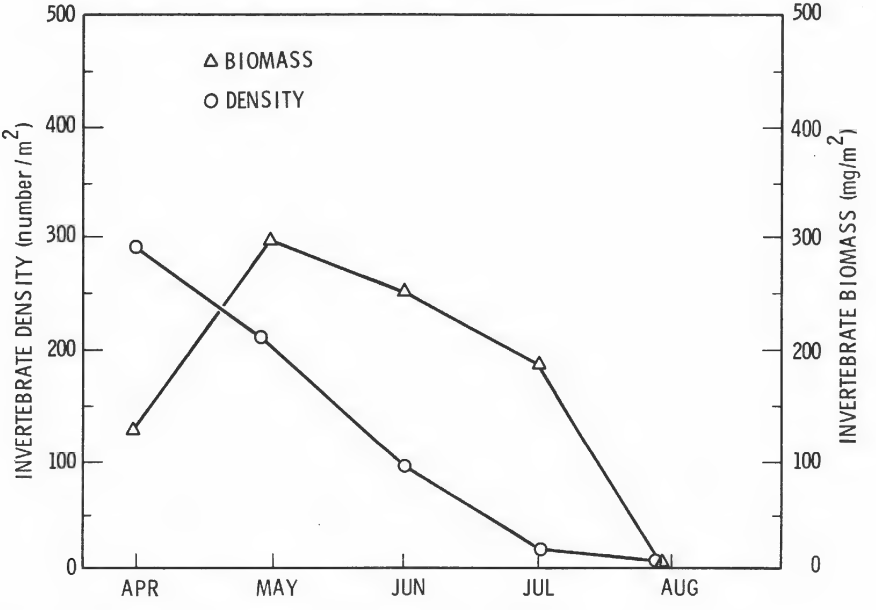

Figure 1. Seasonal distribution of estimated density and biomass.

may have been earlier. A steady decline in density progressed into the summer months, reaching a low point during August. Estimated biomass followed a similar trend, peaking in May and declining through summer with the minimum value recorded in August. These patterns approximate the live plant biomass trend; peak biomass values for green vegetation occur during April or May and then decline with the onset of summer drought conditions (Uresk, pers. comm.). Little green vegetation remains

after the first of July. This fact suggests that the dominant invertebrate groups, in terms of biomass and density, are correlated with the green growth period of early spring.

The taxonomic composition of the invertebrate fauna is shown in Table 1, expressed as percentages of density and biomass. The most abundant invertebrates were mites, beetles, and thrips. The mites were largely members of the family Tetranychidae, a group that feeds on green vegetation. Their life cycle would be expected to be closely attuned to the availability of host plants. There was one abundant beetle family present, the Tenebrionidae, or darkling beetles. They are generally regarded as omnivores (Hewitt *et al.,* 1974) and probably do not require a diet of green vegetation because they are able to feed on detritus. Darkling beetles were most abundant during the months of May and June, with 54 and 34 individuals per m^2 respectively—mostly larvae. The Thysanoptera (thrips) were the third largest contributor to total invertebrate density (Table 1). Thrips are small, frequently overlooked insects. Most are phytophagous and occur on the foliage and in flower heads of various plants.

TABLE 1. Taxonomic distribution (%) of invertebrate density and biomass.

Taxa		Density	Biomass
		. . . . . %	
Coleoptera	(Beetles)	18	51
Diptera	(Flies)	4	6
Lepidoptera	(Butterflies and moths)	<1	7
Araneida	(Spiders)	1	3
Hymenoptera	(Ants, bees, wasps)	8	7
Acari	(Mites)	37	<1
Homoptera	(Cicadas, aphids, etc.)	1	<1
Hemiptera	(Bugs)	8	3
Thysanoptera	(Thrips)	15	1
Psocoptera	(Book lice)	7	<1
Orthoptera	(Grasshoppers)	<1	20
Chilopoda	(Centipedes)	<1	<1

Two taxa, beetles and grasshoppers, accounted for 71 percent of the total estimated invertebrate biomass (Table 1). None of the other 10 taxa represented over 7 percent of the total biomass values. Grasshoppers are occasionally very abundant in this type of community (Rogers and Uresk, 1974), but were present in low numbers during this study. Their relatively large size, however, made them a significant biomass contributor.

An analysis of the trophic distribution of invertebrate density and biomass is shown in Table 2. The herbivore and omnivore groups were the two most important trophic levels, in terms of both density and biomass. The tissue and sap feeders comprised 28 and 24 percent of the total herbivore density, and pollen- and nectar-feeding insects consisted of only 4 percent. There were few flowering plants inhabiting the cheatgrass community, so the paucity of pollen and nectar foragers was expected and is consistent with our field observations. The percent biomass value for pollen and nectar feeders was higher (19 percent) than the density value, mainly resulting from the presence of a few large adult moths.

TABLE 2. Trophic distribution (%) of invertebrate density and biomass.

Trophic Level	Density	Biomass
	. . . . . %	
Herbivore	56	47
Tissue	28	24
Sap	24	4
Pollen & Nectar	4	19
Predator	8	4
Omnivore	34	48
Fungivore	<1	<1
Unknown	<1	<1

Conclusions

Our data show that in an old-field cheatgrass community: (1) invertebrate populations reach maximum density and biomass early in the season (April, May), correlated with peak biomass of green vegetation; (2) the most abundant invertebrate taxa present are mites, beetles, and thrips; (3) beetles and grasshoppers are the largest contributors to invertebrate biomass; and (4) herbivores and omnivores are the largest trophic groups in terms of both density and biomass. We do not know how invertebrate density and biomass in cheatgrass communities compare to those for more pristine communities in the surrounding area. These comparisons are planned as the data become available.

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Literature Cited

Hewitt, G. B., E. W. Huddleston, R. J. Lavigne, D. N. Ueckert, and J. G. Watts. 1974. Rangeland Entomology. Range Sci. Ser. No. 2. Soc. for Range Mgmt., Denver, Colorado. 127 pp.

Rickard, W. H. 1972. Rattlesnake Hills Research Natural Area. *In:* J. F. Franklin, F. C. Hall, C. T. Dyrness, and C. Maser (eds.). Federal Research Natural Areas in Oregon and Washington. A Guidebook for Scientists and Educators. Pacific Northwest Forest and Range Exp. Sta., Portland, Oregon. 498 pp., illus.

Rogers, L. E., and D. W. Uresk. 1974. Food plant selection by the migratory grasshopper *(Melanoplus sanguinipes)* within a cheatgrass community. Northw. Sci. 48:230-243.

————, R. L. Buschbom, and C. R. Watson. 1977. Length-weight relationships of shrub-steppe invertebrates. Ann. Entomol. Soc. Amer. 70:51-53.

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Herpetological Survey at the Trojan Nuclear Plant, Oregon[1]

Abstract

This paper discusses the findings of a herpetological survey conducted at the Trojan Nuclear Plant, Columbia County, Oregon, from May 1972 through August 1973. Drift fences with pitfalls, night-lighting, and field observations were conducted for the purpose of ascertaining relative abundance. A permanent 750 m^2 plot was searched for snakes to yield data on biomass per unit area. There are apparently no other published records of the reptiles and amphibians of Columbia County.

Introduction

A field survey of the reptiles and amphibians inhabiting the environs of the Trojan Nuclear Station site in Columbia County, Oregon, was conducted from May 1972 through August 1973. The purpose was to provide general information on their relative abundance and habitat preferences.

The secretive nature of the cold-blooded vertebrates has resulted in an incomplete picture of their geographic and ecologic distribution in Oregon. We found no published records of specimens collected in Columbia County. These data are necessary in order to assess fully the position which reptiles have in the environment and to identify rare and/or endangered species.

The Trojan property consists of approximately 243 ha surrounding the newly constructed nuclear power station. The area borders the west shoreline of the Columbia River and includes pond, forest, and grassy meadow habitats. The most abundant tree species on well-drained soils is Douglas-fir, *Pseudotsuga menziesii* (Rickard, 1975). Winters are moist with temperatures seldom below freezing; summer temperatures are moderate with many days without measurable rainfall. Average January temperatures are 7°C max. and 0°C min. Average July temperatures are 26°C max. and 10°C min. The average annual rainfall is 114.6 cm.

Methods Employed

General field collections were made by searching preferred reptile or amphibian habitats; i.e., under stones, logs, other surface debris, and by night-lighting roadways and ponds. These observations were supplemented by pitfall traps, each 35 cm in diameter and

[1] This study was supported by the Portland General Electric Company, Portland, Oregon 97025.

41 cm deep, spaced at 5 m intervals along a 30 m long by 40 cm high strip of drift fence. The fence was a strip of 6 mm mesh hardware cloth. The study site was on a steep, north-facing slope well stocked with mature Douglas-fir trees and an understory of sword fern *(Polystichum munitum)*. The pitfalls were checked 19 times between 23 January and 19 July 1973. Gibbons and Bennett (1974) used a similar drift-fence technique in South Carolina and found it to be a valuable method for studying the population dynamics of migrating amphibians.

A special 750 m^2 (5 x 150 m) plot was staked out in a dry, grassy meadow habitat that was cut annually for hay. The plot was searched for snakes. Startled snakes were hand captured and released after identifying individuals to species, weighing, and recording total length and tail length. Individual snakes were marked using ink tatoos on ventral scales (Woodbury, 1953). The plot was searched in mid-morning on 27 September 1972, and 18 July and 14 August 1973.

Results and Discussion

Six species of newts and salamanders were found on the Trojan property. These were northwestern salamander *(Ambystoma gracili)*, long-toed salamander *(A. macrodactylum)*, rough-skinned newt *(Taricha granulosa)*, Dunn's salamander *(Plethodon dunni)*, western red-backed salamander *(Plethodon vehiculum)*, and Ensatina *(Ensatina escholtzi)*. Three frog species were observed: bull frog *(Rana catesbeiana)*, red-legged frog *(Rana aurora)*, and pacific tree frog *(Hyla regilla)*. The bull frog is not native to the region, having been introduced to Oregon from the eastern United States. The only lizard observed was the northern alligator lizard *(Gerrhonotus coeruleus)* and the only turtle seen was the painted turtle *(Chrysemys picta)*. The common garter snake *(Thamnophis sirtalis)* and the northwestern garter snake *(T. ordinoides)* were the only snake species sighted. Gordon (1939), Anderson and Slater (1941), Graf *et al.* (1939), and Stebbins (1953) provide distributional lists which closely match our findings. Their lists, however, were based on specimens collected or observed in areas outside of Columbia County.

Pitfalls, supplemented by a drift fence, were efficient collectors of newts and salamanders. Rough-skinned newts, long-toed, northwestern, and red-backed salamanders, ensatina, and red-legged frogs were captured (Table 1). The amphibian most often

TABLE 1. Total number of amphibians collected in pitfall traps during the period 23 January to 19 July 1973.

Species	January 23 to February 27	February 28 to March 26	March 27 to April 24	April 25 to May 20	May 21 to June 19	June 21 to July 19
Rough-skinned Newt	35	6	2	0	3	2
Long-toed Salamander	1	0	1	0	0	0
Northwestern Salamander	1	1	1	0	1	0
Western Red-backed Salamander	0	0	1	0	0	0
Ensatina	1	1	0	0	0	0
Red-legged Frog	0	0	2	0	0	1
Total	38	8	7	0	4	3

found in the pitfalls was the rough-skinned newt, 48 in all. Pitfall catches were high in winter then declined with the onset of warmer, dry, summer weather. Gordon (1939) indicated that the genus Taricha is common in the area we studied but stated the taxonomic status of the species present in Columbia County is as yet uncertain. He further stated that three species of Ambystoma *(A. gracili, A. macrodactylum, A. tigrinum)* are probably more common in the lowlands than in the surrounding mountains. We did not observe *Ambystoma tigrinum* in our study area.

Fifty-four garter snakes were captured on the grassy meadow plot (Table 2). Eighteen were common garter snakes *(Thamnophis sirtalis)* and 36 were northwestern garter snakes *(T. ordinoides)*.

TABLE 2. Hand captures of garter snakes on a transect line, Trojan Site, Columbia County, Oregon.

Sept. 27, 1972			July 18, 1973					August 14, 1973				
ID	SP	Wt.	ID	SP	Wt.	L	Tail	ID	SP	Wt.	L	Tail
1	N	2.5	103	N	16.5	384	84	122	N	35.0	514	110
2	C	50.0	104	N	5.0	260	55	123	N	26.0	495	110
3	C	36.0	105	N	32.0	495	113	124	C	28.0	495	115
4	N	6.5	106	N	18.0	429	113	125	C	36.0	514	92
5	C	3.0	107	N	7.5	309	74	126	N	14.0	394	90
6	N	19.0	108	N	24.5	466	113	127	C	21.0	457	114
7	N	5.0	109	N	30.5	478	111	128	C	19.0	360	60
8	N	3.0	110	N	23.0	459	104	129	N	30.0	406	—
9	C	6.0	111	C	18.0	429	111	130	N	27.0	495	130
10	C	20.0	112	N	18.5	423	100	*120	C	38.0	603	153
11	N	30.0	113	C	19.0	413	105					
12	C	117.0	114	N	37.0	453	† 67	Total Wt.		274.0		
13	C	68.0	115	N	33.5	456	85					
14	N	21.5	116	N	20.0	423	110					
15	N	18.0	117	C	13.0	325	76					
16	N	17.0	118	N	14.0	355	94					
17	N	3.0	119	C	50.0	613	168					
18	N	7.0	120	C	39.0	570	141					
19	N	2.0	121	C	23.0	426	69					
20	C	81.0										
21	N	2.5	* 6	N	25.0	441	123					
22	N	27.0	Total Wt.		467.0							
23	N	2.0										
24	N	22.5										
25	N	2.0										
26	N	4.0										
Total Wt.		565.5										

LEGEND

C = Common garter snake
N = Northwestern garter snake
ID = Identification number
Wt = Grams
L = Total length in mm
Tail = Tail length in mm

* = recapture
† = broken tail

Northwestern garter snakes had a mean body weight of 17.1 g SE ± 1.8, ranging from 2.0 to 37.0 g. The common garter snakes were heavier, having a mean body weight of 36.1 g SE ± 6.0, ranging from 3.0 to 117 g.

A common garter snake captured and marked in September 1972 was caught again in 1973; its weight had increased from 19 to 25 g. Another common garter snake marked in July 1973 was captured in August; its weight had declined slightly from 39 to 38 g.

The length of common garter snakes ranged from 325 to 615 mm, tails ranging from 60 to 168 mm. Northwestern garter snakes were shorter and ranged in length from 260 to 514 mm, with tails ranging from 55 to 113 mm. Hebard (1950) examined 533 specimens of *Thamnophis* collected from King County, Washington, and also noted that common garter snakes were longer and heavier bodied than the northwestern garter snake. The greatest biomass of garter snakes on the plot was measured in July 1972—0.7 g/m^2 live weight.

About 40 acres of the Trojan site are occupied by railroads, roadways, buildings and structures, parking lots, and other construction. The remainder of the site continues to be biologically productive and now serves as a refugium for herptofauna. With the exception of the bull frog, herptiles have little or no direct use to humans as a food and some species are secretive and seldom seen by people; nevertheless, they do provide a food base for carnivorous fish and the great blue heron.

Literature Cited

Anderson, O I., and J. R. Slater. 1941. Life Zone Distribution of the Oregon Reptiles. Occasional Papers. College of Puget Sound, Tacoma, Washington. 10 pp.

Gibbons, J. W., and D. H. Bennett. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974(1):236-243.

Gordon, K. 1939. The Amphibia and Reptilia of Oregon. Oregon State College, Oregon State Monographs. Studies in Zoology. No. 1. 82 pp.

Graf, W., S. G. Jewett, Jr., and K. L. Gordon. 1939. Records of amphibians and reptiles from Oregon. Copeia 1939(2):101-104.

Hebard, W. B. 1950. Relationships and variation in the garter snakes, genus Thamnophis, of the Puget Sound region of Washington State. Herpetologica 6(4):97-101.

Rickard, W. H. 1975. Litterfall in a Douglas-fir forest near the Trojan Nuclear Power Station, Oregon. Northw. Sci. 49:183-189.

Stebbins, R. C. 1953. Amphibians and Reptiles of Western North America. McGraw-Hill Book Company, New York, New York. 536 pp.

Woodbury, A. M. 1953. Methods of field study in reptiles. Herpetologica 9:87-92.

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Occurrence of a Wild Albino Chinook Salmon (Oncorhynchus tshawytscha) in the Columbia River

Abstract

A 42 mm juvenile albino chinook salmon *(Oncorhynchus tshawytscha)* was captured in the Columbia River near Richland, Washington, on April 20, 1975.

Albinism has been reported in wild salmonids, genus *Salvelinus,* (Blackett and Armstrong, 1945; Allin, 1965) and has been found in Northwest fish hatcheries that raise rainbow trout, *Salmo gairdneri,* coho salmon, *Oncorhynchus kisutch,* and chinook salmon, *O. tshawytscha* (Hager, Washington Department of Fisheries, pers. comm.). However, the abnormality has not been reported for natural chinook salmon populations (Dawson, 1964, 1966, 1970), with the exception of a possible albino adult chinook observed in a fish ladder at Pelton Dam in the Deschutes River, Oregon, in 1961 (Leonards and Madden, 1963).

We collected a 42 mm (fork length) albino chinook salmon from the shoreline of the Columbia River 65 km above Richland, Washington, during seining operations, on 20 April 1975. Since hatchery chinook from upriver locations are released later in the spring and are larger (Anderson, Washington Department of Fisheries, pers. comm.), the fish probably originated from natural spawning populations. Immediately adjacent areas contain up to 30 percent of the estimated fall chinook redds located in the Hanford Reach (Watson, 1970).

After initial examination, the albino was preserved in 10 percent formalin. The specimen was devoid of all normal coloration, appearing pale white with pinkish eyes. Scale formation was not yet evident. Detailed microscopic examination showed no melanistic pigmentation among fin rays or on the ventral body surface. Scattered melanophores were detectable, however, on each operculum and along the dorso-lateral body surface. The salmon did not differ morphologically or meristically from other wild chinook captured in this area. Figure 1 compares markings of the albino specimen with a normally pigmented chinook captured and preserved at the same time.

We have examined over 49,000 wild 0-age chinook salmon taken in the central Columbia River from 1973-1976. No other case of abnormal coloration has been detected. The low incidence of albinism in natural populations may reflect the albino's

lack of protective coloration, as well as weakened eyesight, increasing its vulnerability to predators.

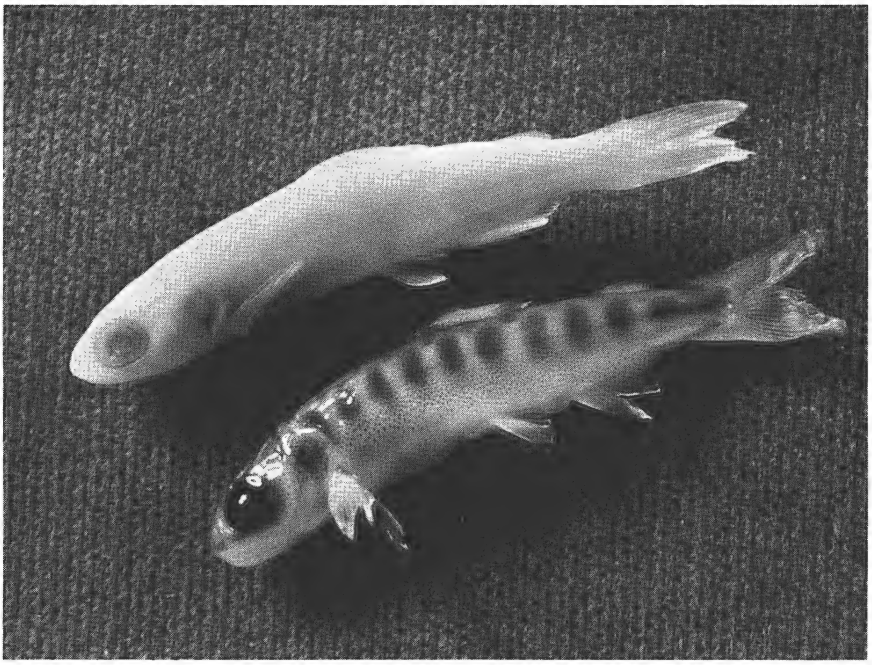

Figure 1. Comparison of markings between the albino chinook salmon fry and a normally pigmented chinook salmon fry.

Acknowledgments

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Literature Cited

Allin, A. E. 1945. Another albino lake trout. Copeia 1945 (1):55.

Blackett, R. G., and R. H. Armstrong. 1965. Collection of two abnormal Dolly Varden: one with two dorsal fins, the other with incomplete pigmentation. Trans. Am. Fish. Soc. 94(4):408-409.

Dawson, C.E. 1964. A bibliography of anomalies of fishes. Gulf Res. Rep. 1(6):308-309.

————. 1966. A bibliography of anomalies of fishes. Suppl. 1. Gulf Res. Rep. 2(2):169-176.

————. 1970. A bibliography of anomalies of fishes. Suppl. 2. Gulf Res. Rep. 2(2):205-239.

Leonards, L., and E. Madden. 1963. Possible albino adult chinook observed. Res. Briefs. Ore. Fish Comm. 9(1):67.

Watson, D. G. 1970. Fall Chinook Salmon Spawning in the Columbia River near Hanford 1947-1969. BNWL-1515, Battelle Northwest, Richland, WA. 45 pp.

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Balsamorhiza rosea **and** Eriogonum thymoides **in Benton County, Washington, 1976**[1]

Abstract

The distribution of *Balsamorhiza rosea* and *Eriogonum thymoides,* plants on the Smithsonian Institution's Threatened and Endangered Species List, was examined in Benton County, Washington, during the spring of 1976. Both species occupied stony, basaltic substrates on ridge crests. Apparent hybridization between *B. rosea* and *B. careyana* is described.

The major man-induced threat to ridge crest habitats is the building of television and radio communication towers and their associated access roads. Small plant populations could be extirpated by these construction activities if some provision is not made for conservation of habitat.

Introduction

Scientific and educational interest in preserving and protecting representative habitats of native plants in the United States is growing as the demand for converting wild acreages to agricultural, residential, and industrial use increases. The protection of wild habitats on federally owned lands in the Pacific Northwest for scientific and educational purposes has been pioneered by the United States Forest Service (Franklin *et al.,* 1972). There is also a renewed interest in providing protection for plant species whose populations are so low that they are in danger of becoming extinct. One of the initial steps in providing protection is the preparation of a list of species believed to be in need of protection. Such a list has been published by the Smithsonian Institution (1974) and shows two Washington shrub-steppe species, *Balsamorhiza rosea* Nels. and Macbr. (Compositae) and *Eriogonum thymoides* Benth. (Polygonaceae), as being "threatened."

This paper provides recent information concerning the occurrence of these plants in Benton County, Washington, a rapidly developing area for irrigated agriculture and industry.

History

The first list of vascular plant species of Benton County was published by St. John and Jones (1927). These authors cite herbarium specimens from the Rattlesnake Hills for both *E. thymoides* and *B. rosea.*

Hitchcock *et al.* (1955-69) describe the distribution of *B. rosea* from only three

[1] This work was performed by Battelle-Northwest for the Energy Research and Development Administration under Contract E(45-1)-1830.

localities, all in south-central Washington, and the type locality is indicated as the Rattlesnake Hills. *Eriogonum thymoides* is described as being widely distributed in the shrub-steppe region east of the Cascade Mountains in Washington and Oregon, extending eastward into Idaho.

Weber (1946) collected specimens of *B. rosea* from a rocky hilltop southwest of the town of Touchet in adjacent Walla Walla County and St. John (1956) described its occurrence in Spokane County as local.

Methods

Because *B. rosea* and *E. thymoides* are both restricted to the very stony soils of ridge crests, the search was restricted to ridges. Visits were made by car and foot to the prominent ridges in Benton County in May 1976 when plants were in flower (Fig. 1).

A suspected hybrid of *B. rosea* x *B. careyana* was selected for study. Leaves and flowering stalks of ten plants were counted and the longest leaf of each plant was collected and pressed.

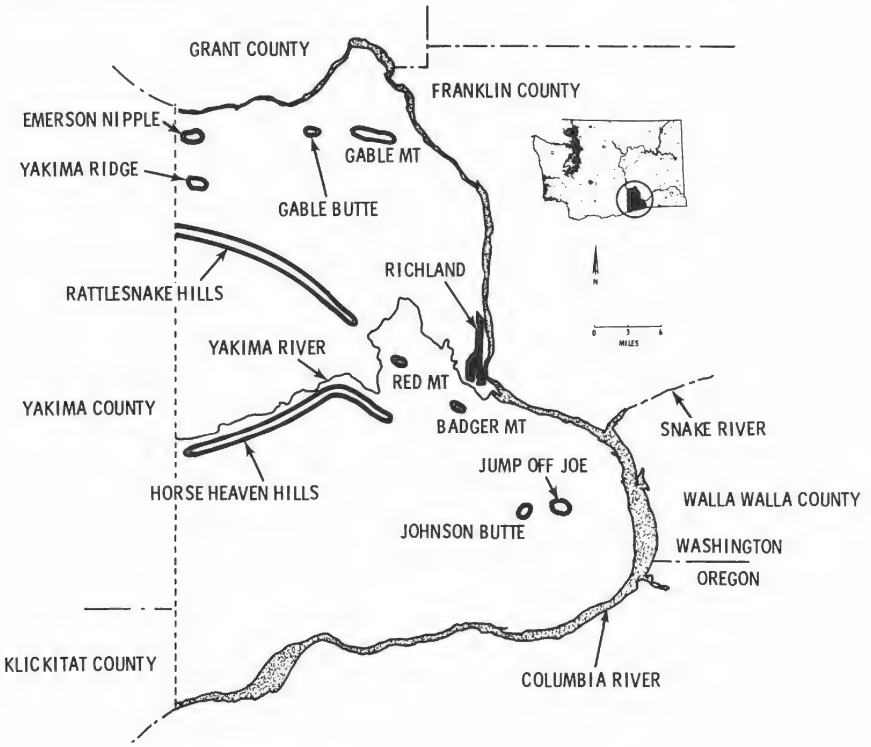

Figure 1. Map of Benton County, Washington, showing prominent ridges searched for populations of *Balsamorhiza rosea* and *Eriogonum thymoides*.

Results and Discussion

Occurrence in Benton County

The locations of plant populations found in Benton County are shown in Table 1. *Eriogonum thymoides* is probably restricted to the ridge crest habitats on Emerson Nipple, Yakima Ridge, and the Rattlesnake Hills. *Balsamorhiza rosea* was found on the Rattlesnake Hills, Jump Off Joe Butte, Badger Mountain, and Red Mountain; but it was especially abundant in the Horse Heaven Hills. *Eriogonum thymoides* was less widely distributed than *B. rosea,* and it was also less abundant when the two species occupied the same habitat. For example, a site in the Rattlesnake Hills showed that *B. rosea* plants were 45 times more numerous than *E. thymoides* (density of 18/m^2 compared to 0.4/m^2).

TABLE 1. Occurrence of *B. rosea* and *E. thymoides* in Benton County, Washington.

Location	Elevation (maximum) meters	Taxa	
		B. rosea	*E. thymoides*
Rattlesnake Hills	1093	+	+
Emerson Nipple	977	—	+
Jump Off Joe	923	+	—
Johnson Butte	623	—	—
Horse Heaven Hills	624	+	—
Yakima Ridge	508	—	+
Badger Mountain	458	+	—
Red Mountain	428	+	—
Gable Mountain	339	—	—

\+ Present
— Not observed

Daubenmire (1970) analyzed an undisturbed *Eriogonum sphaerocephalum* low shrub stand at 949 m elevation in the Rattlesnake Hills. His data show that total canopy cover was 49 percent. Perennial grasses provided 35 percent of the canopy cover, low shrubs 8 percent, perennial forbs 4 percent, and annual plants only 2 percent. *Eriogonum sphaerocephalum, Haplopappus stenophyllus,* and *Erigeron linearis* were the important low shrubs, *Poa secunda* the important grass, and *Lupinus sulfureus, Arenaria dimorpha, Lomatium gormanii* were the most abundant perennial forbs. *Bromus tectorum* was the most abundant annual. Only 20 species were recorded on 4 m^2 of examined ground spread over forty 0.1 m^2 study plots. *Balsamorhiza rosea* and *B. careyana* were reported as occuring near but not on the study plots, and *E. thymoides* was not recorded.

The highest elevation observed to support *B. rosea* colonies was 1093 m and the lowest 428 m (Table 1). Generally, *B. rosea* extended to lower elevations on steep north-facing slopes than it did on steep south-facing slopes. The population of *B. rosea* is clearly disjunct with the largest contiguous stands in the Horse Heaven and Rattlesnake Hills. Some colonies comprising in total a few acres or less were located on the summits of Red Mountain, Jump Off Joe Butte, and Badger Mountain.

Man's Influence on Ridge Crest Habitats

Deep, stone-free soils of surrounding ridges are intensively managed for dryland wheat

Figure 2. Photographs of *B. rosea* (upper), *B. careyana* (lower), and suspected hybrid plants (middle). A leaf of *B. careyana* is shown with *B. rosea* as an indication of relative plant size.

or irrigated crops and orchards so that only the ridge crests support islands of native vegetation surrounded by many acres under agricultural management.

The most obvious man-induced disturbances currently being imposed on ridge crest plant communities today are the construction of radio and television communication towers, their supporting buildings, and the service roads leading to the facilities (Fig. 2). Although the acreage occupied by such facilities is not very large, neither is the total acreage occupied by *B. rosea* and *E. thymoides*. Even when small parcels of land are pre-empted, the population on a particular site can be substantially reduced. At this time, there is no special protection provided for ridge crest habitats except in the portions of Rattlesnake Hills located within the boundaries of the Arid Lands Ecology (ALE) Reserve, a tract of land maintained in a wild condition by the Energy Research and Development Administration as a site for scientific and educational study.

Ridge crest plant species have probably been little affected by past agricultural use. In the future, agriculture will probably have little direct impact on these species because the soil is unsuitable for cultivation. However, these communities are subjected to drift of aerially applied chemical herbicides when nearby agricultural fields are sprayed. The impact of this herbicide drift on ridge crest plant communities has not been investigated.

Temperature Gradients

Although soil stoniness appears to be a necessary component of *B. rosea* habitat, other abiotic factors are also important. Stony soils often occur on low altitude ridges, but these were not observed to support *B. rosea*. This finding suggests that climate plays an important role in determining whether *B. rosea* can successfully exist on otherwise superficially suitable substrates. Average daily maximum and minimum air temperatures are shown in Table 2. These temperatures were collected from thermographs in standard weather bureau shelters placed along an elevational gradient in the Rattlesnake Hills. *Balsamorhiza rosea* was not found on the Rattlesnake Hills where the average maximum air temperature at this time of year exceeded 19°C. It should be noted that ground level temperatures are often much higher (Hinds and Rickard, 1972). Soil water is an important consideration in plant growth, but stony soils are a difficult media in which to obtain meaningful measurements.

Balsamorhiza careyana is common in Benton County, grows on deep soils at the lowest altitudes, and extends to the highest altitudes as long as the soil profile remains partly stone-free. *Balsamorhiza careyana* often grows within a few meters of *B. rosea*

TABLE 2. Average air temperatures along an altitudinal gradient in the Rattlesnake Hills during the period April 15-May 15 inclusive for 1973, 1974, and 1975.

Station	Elevation (m)	Elevation (ft)	1973 Mx	1973 Mn	1974 Mx	1974 Mn	1975 Mx	1975 Mn	Average Mx	Average Mn
Observatory	1075	(3530)	12.9	3.8	*13.1	*4.5	*11.4	*3.9	12.7	4.0
Anderson Rim	884	(3000)	15.9	5.3	11.4	2.2	14.0	2.5	13.8	3.3
Upper Snively	533	(1750)	*20.7	*6.4	*19.3	*6.4	*15.8	*5.0	18.5	5.9
Lower Snively	323	(1060)	*22.3	*8.6	19.4	7.6	18.2	6.0	19.9	7.5
Meteorology Station	223	(730)	22.8	6.4	20.6	6.4	20.0	5.4	21.1	6.1

* Data missing in part due to instrument failure.

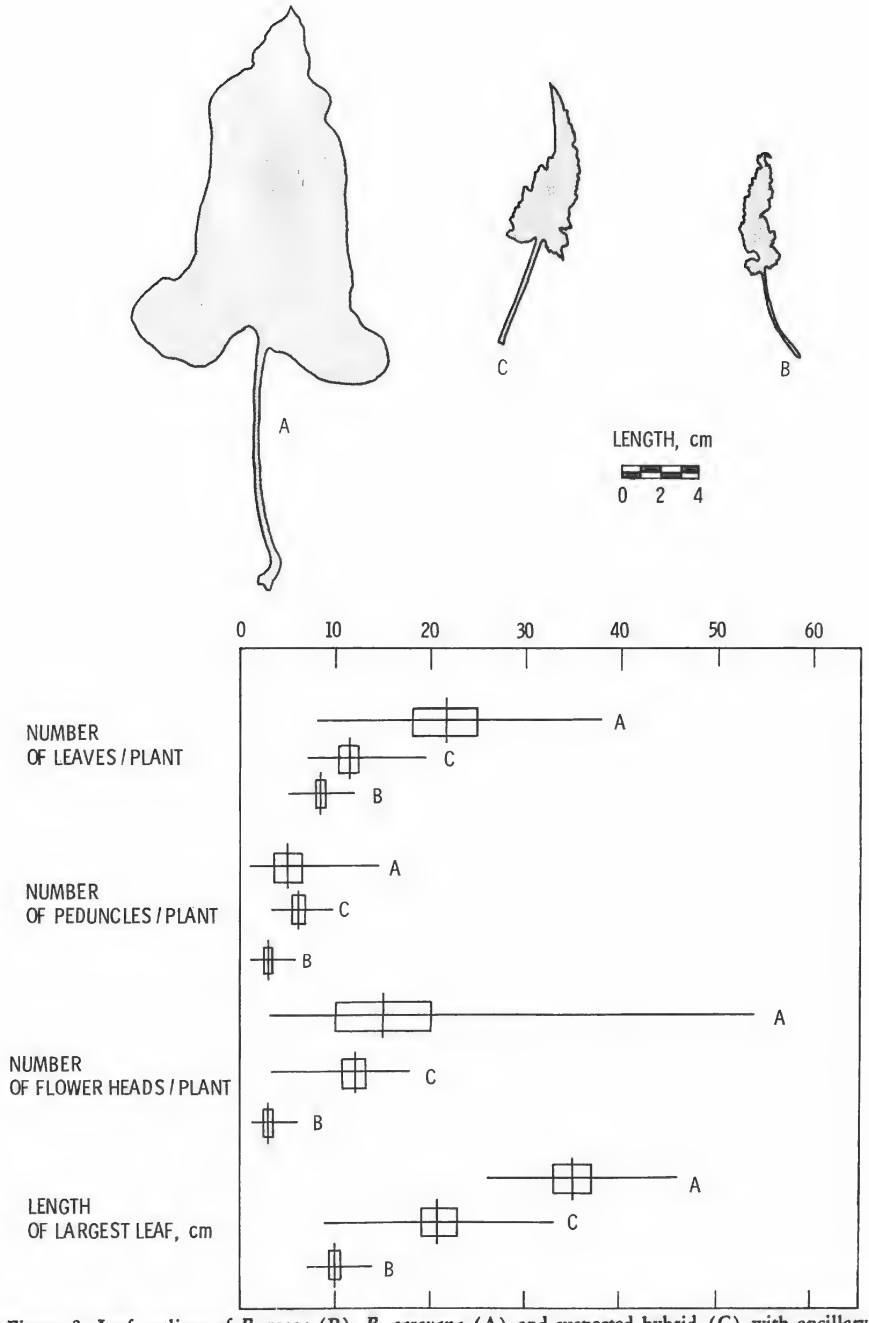

Figure 3. Leaf outlines of *B. rosea* (B), *B. careyana* (A) and suspected hybrid (C) with ancillary anatomical measurements showing range and mean values and the standard error of the mean, n = 10.

habitat. When this growth occurs, plants that appear to be hybrids sometimes result, and they occupy a narrow zone between the two distinctive populations.

Hybridization

At maturity, *B. rosea* is a much smaller plant than *B. careyana* (Fig. 3). *Balsamorhiza rosea* is dark green in leaf color as compared to light green for *B. careyana.* At maturity,

Figure 4. Communication facilities located on the crest of the Rattlesnake Hills. These kinds of facilities pre-empt scarce ridge crest plant habitat.

the petals of *B. rosea* take on a reddish coloration that is absent in *B. careyana.* The leaves and peduncles of *B. rosea* tend to be prostrate while those of *B. careyana* are more upright. Tracings made from pressed leaves of *B. rosea* and *B. careyana* are shown in Fig. 4 along with data showing the number of leaves per plant, number of peduncles per plant, number of flowering heads per plant, and the length of the largest leaf. The suspected hybrid is usually intermediate in regard to these measurements.

Ownbey and Weber (1943) have described suspected hybrids between *B. careyana* and *B. deltoidea, B. careyana* and *B. hirsuta* var. *lagocephala, B. careyana* and *B. hookeri, B. careyana* and *B. sagittata, B. careyana* and *B. serrata, B. sagittata* and *B. hirsuta* var. *lagocephala, B. sagittata* and *B. hispidula, B. sagittata* and *B. hookeri, B. sagittata* and *B. incana, B. sagittata* and *B. serrata.* They have suggested that hybridization in wild populations of *Balsamorhiza* could be treated experimentally to lead to a better understanding of speciation in plants. Weber (1946) determined the haploid number of *B. rosea* as 19 and the diploid number of *B. careyana* as 38.

Aggressiveness

Balsamorhiza rosea populations occupy relatively little total acreage and thus are vulnerable to extirpation or perhaps extinction by man's activities. However, it seems to be aggressively invading the disturbed ground, associated with mechanical scraping of roadsides. This aggressiveness could enhance its ability to survive future soil disturbances. *Eriogonum thymoides* did not seem to have this same ability, but the opportunities to observe seedling establishment of *E. thymoides* were also much less frequent.

Conclusion

Balsamorhiza rosea and *Eriogonum thymoides* occupy relatively little acreage in Benton County, Washington, but the present-day distribution is probably much like it was before man began agricultural and industrial development more than a hundred years ago. The major threat to habitat today is road building, off-road vehicular traffic, and the choice of ridge crest locations for communication transmission facilities. Future development of ridge crest sites may involve the building of wind stations to generate electricity.

Agricultural development has had little apparent impact on ridge crest sites because of poor quality soil, but the impact of herbicide drift on these ridge crest plant communities has not been investigated.

Literature Cited

Daubenmire, R. 1970. Steppe Vegetation of Washington. Wash. State Agr. Ext. Bull. 62. 131 pp.

Franklin, J. F., F. C. Hall, C. T. Dyrness, and C. Maser. 1972. Federal Research Natural Areas in Oregon and Washington: A Guidebook for Scientists and Educators. USDA For. Serv. Pac. Northwest For. and Range Exp. Stn., Portland, OR. 498 pp., illus.

Hinds, W. T., and W. H. Rickard. 1968. Soil temperatures near a desert shrub. Northw. Sci. 42:5-13.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1955-1969. Vascular Plants of the Pacific Northwest. 5 Vols. University of Washington Press, Seattle.

Ownbey, M., and W. A. Weber. 1943. Natural hybridization in the genus *Balsamorhiza.* Am. J. Botany 30:179-183.

St. John, H., and G. N. Jones. 1927. An annotated catalogue of the vascular plants of Benton County, Washington. Northw. Sci. 2:73-93.
————. 1956. Flora of Southeastern Washington and Adjacent Idaho. State College of Washington Press, Pullman. XXV + 561 pp.
Smithsonian Institution, 1974. Report on Endangered and Threatened Plant Species of the United States. Wash., D.C., Smithsonian Institution. 200 pp.
Weber, W. A. 1946. A taxonomic and cytological study of the genus *Wyethia,* family Compositae, with notes on the related genus *Balsamorhiza.* Am. Midl. Nat. 35:400-452.

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Bottom Fauna as an Indicator of Lake Typology in Flathead Lake, Montana

Abstract

The horizontal and vertical distribution of the bottom fauna of Flathead Lake, Montana, is discussed. The benthic fauna of the lake suggests oligochaetes widespread at all depths. Larvae of *Stictochironomus* and *Procladius* comprised almost 75 percent of the chironomid fauna. The presence of species of *Heterotrissocladius, Monodiamesa,* and *Protanypus* reflects the existence of some ultraoligotrophic areas in the lake. There were no indications of eutrophic conditions. The evidence of widespread oligotrophic conditions supports previous evidence acquired from limnological studies.

Introduction

The purpose of this research was to describe the chironomid and oligochaete fauna of Flathead Lake, Montana, to investigate the depth distribution of the benthos, and to use the Chironomidae in a discussion of the trophic typology of this lake. Flathead Lake has been under intensive limnological investigation for several years and much of this research has been reviewed and consolidated by Gaufin *et al.* (1976). However, the investigation by Young (1935) is the last published report on the benthos of Flathead Lake.

The use of chironomids as indicators of lake typology was first proposed by Brundin (1949), but this technique has been used only sparingly on North American lakes. Saether (1975c), however, has reviewed this method and its application to North American lakes.

Results of benthic typology studies in the Okanagan Valley, British Columbia, are compared and contrasted with the Flathead Lake fauna (Saether and McLean, 1972). A secondary objective was to add to the present meager knowledge of chironomid and oligochaete zoogeography in western North America.

Study Area

Flathead Lake (Fig. 1) is one of the largest natural freshwater lakes west of the Mississippi River. It lies in Lake and Flathead counties in northwestern Montana at the southern end of the Rocky Mountain Trench and is part of the Columbia River drainage system. The lake is naturally dammed at its southern end by a terminal moraine from the Wisconsin glaciation. Lake levels are regulated between 879 m and 882 m (MSL) by a dam located 7 km downstream of the natural lake outlet. Some of the morphometric data on Flathead Lake are presented in Table 1.

The bottom material is variable throughout the lake. The bays have bottoms of coarse to fine organic matter and the depositional zone off the mouth of the Flathead River is predominately inorganic sediments. The east and west shores have substrates that include varying proportions of sand, gravel, cobble, and boulders.

Methods and Materials

The benthos of Flathead Lake was sampled using a drag dredge towed behind a boat (Fast, 1968). About 37 m (120 ft) of bottom were sampled at each station as the dredge was towed approximately 0.33 m sec^{-1} (1 ft sec^{-1}) along the bottom. Tows were made parallel to bottom contours. A total of 77 tows were made at 22 sampling stations variously located around the lake where depths ranged from 4 m (14 ft) to 55 m (180 ft). Samples of bottom fauna should only be considered as semi-quantitative as a result of the variable nature of the lake bottom and the efficiency of the drag dredge. At the completion of each tow the dredge was pulled to the surface and all organisms were removed and preserved in A.F.A. All sampling was conducted during the summer and fall over a three-year period.

In the laboratory all Chironomidae and Oligochaeta were mounted on glass slides using CMC-10 non-resinous mountant. All mounted specimens were allowed to air dry and clear for one week; after this time period, they were examined under a compound microscope and identified. Other larger organisms were examined under a dissecting microscope.

Results

Chironomids were collected at all depths sampled, but oligochaetes were absent from some samples (Table 2).

Individuals of the families Lumbriculidae and Naididae were not common in the samples. Three naidid taxa were collected at 12 m depth and one was taken at 17 m. Tubificids were evident through the entire depth range. Only one identifiable specimen of *Ilyodrilus templetoni* was taken at 12 m. *Limnodrilus hoffmeisteri* was found at depths of 21-55 m. A total of 236 oligochaetes were collected in 276 minutes of dredge time ecompassing some 40 sampling locations (Table 2).

The chironomid fauna was represented by 1677 individuals separable into 25 taxa (Table 2). All taxa were present in the 4-21 m depths, but only seven taxa were taken in the profundal zone (22-55 m). Individuals of *Microchironomus* and *Pagastiella* were confined to the littoral zone (4 m). The greatest sampling effort was expended at the 21 m depth resulting in the greatest number of taxa (15) and individuals (491) taken from that depth.

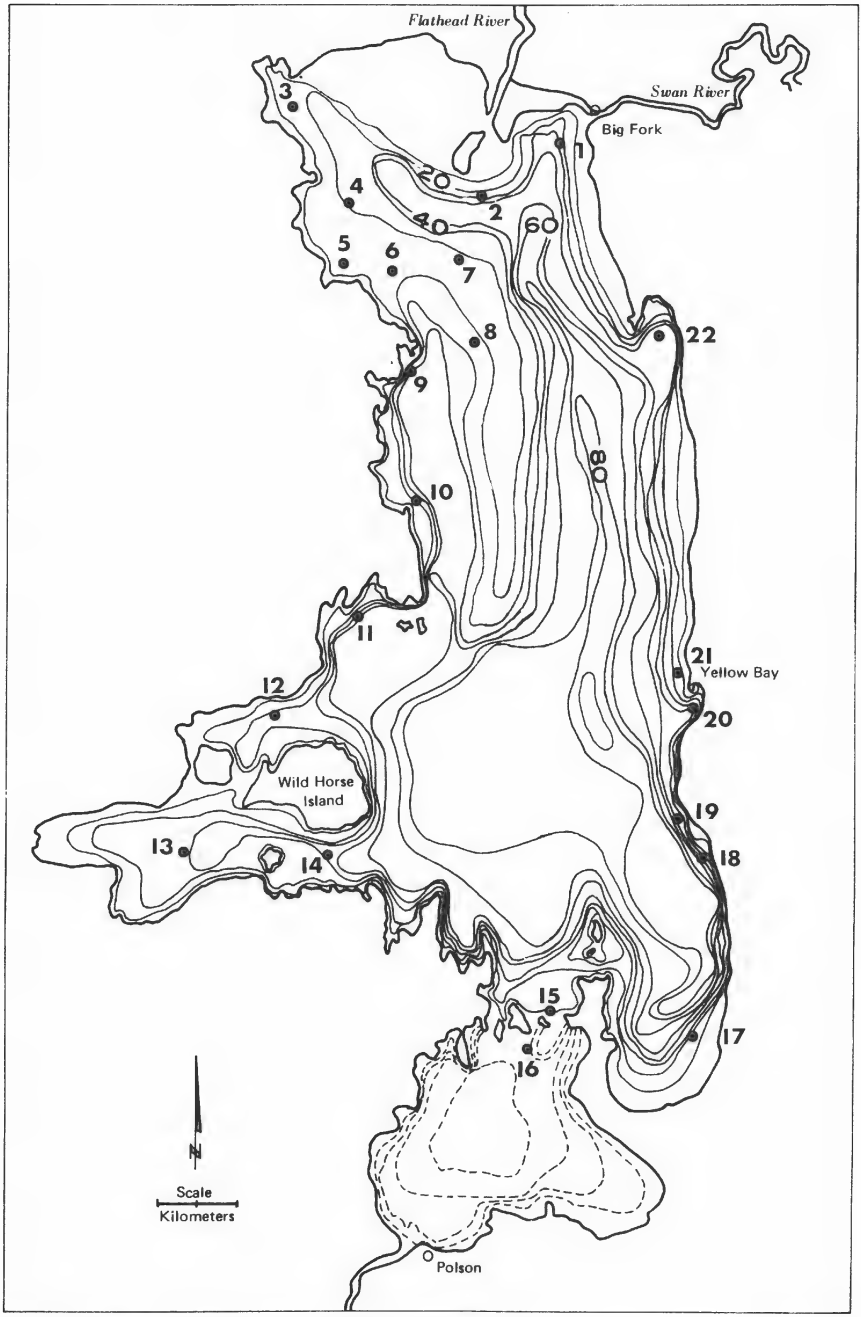

Figure 1. Map of Flathead Lake, Montana, showing bottom contours (meters) and sampling stations.

The genus *Stictochironomus* was the most abundant chironomid collected, comprising 53 percent of the fauna (889 individuals). *Procladius* was the second most abundant taxon with 400 individuals or 23.9 percent of the fauna. In decreasing order of abundance, the other common chironomid taxa included *Chironomus* (93), *Protanypus hamiltoni* (73), *Heterotrissocladius oliveri* (63), and *Pagastiella* (33).

TABLE 1. Morphometric data on Flathead Lake (from Potter and Stanford, 1975).

Area (km^2)	476.6
Drainage (km^2)	18,378.6
Average Annual Discharge (km^3)	10.5
Shoreline (km)	259.7
Maximum Length (km)	43.9
Maximum Breadth (km)	24.9
Maximum Depth (m)	113.0
Mean Depth (m)	32.5
Volume (km^3)	24.9
Mean Water Retention (years)	2.37

Protanypus hamiltoni was distributed at depths ranging from 17 to 47 m. With the exception of a single specimen captured at station 20 on the east shore, all larvae were taken in the northeast quadrant of the lake at stations 3-12. A variety of substrates occurs at these sampling stations.

Heterotrissocladius latilaminus was confined to the littoral-upper profundal zone (9-21 m depth). This species was common in the northern part of the lake (stations 3, 5, 7) and rare elsewhere in the lake (station 20). *Heterotrissocladius oliveri* was found in the 17 to 37 m depth range and its greatest densities were at station 7 and 8 in the depositional region at the mouth of the Flathead River.

Larvae of *Monodiamesa prolibata* preferred the littoral and upper profundal zones (9-21 m) and were found at scattered locations (stations 3, 5, 15, 20) around the lake.

The list of larger macroinvertebrates collected in Flathead Lake, together with their depth distribution, is found in Table 3. Individuals of Hydrazoa and Trichoptera were collected out to 18 m depth, Amphipods to 29 m, and mayflies (Ephemeroptera) to 33.5 m. Only Oligochaeta and Chironomidae were commonly taken at deeper sampling stations.

Discussion

Comparison with Other Western Lakes

Wiederholm (1976) noted that the bottom fauna of Lake Sammamish, Washington, was dominated by chironomids out to his maximum sampling depth of 25 m. The most abundant chironomid collected in this mesotrophic lake was *Chironomus salinarius* (kieff). Eighteen genera of Chironomidae were reported identified from Lake Sammamish, most of which were also found in Flathead Lake.

In mesotrophic-oligotrophic Lake Washington, Washington, Thut (1965) found the benthos dominated by chironomids down to depths of 25 to 30 m, below which oligochaetes dominated. *Chironomus atritibia* was the most abundant benthic chironomid reported.

Although identifications were not recorded to the species level for the genus

TABLE 2. Depth distribution of Oligochaeta and Chironomidae in Flathead Lake.

Depth (m)	4	9	12	17	18	21	22	24	25	26	27	28	29	30	31	34	35	36	37	47	55	
No. Samples	1	2	1	1	2	12	1	1	1	1	2	3	1	1	1	2	1	1	3	1	1	1 = 240
Tow Time (min.)	2	1½	1½	1½	3	22½	1½	1½	1½	3	4	7½	1½	1½	1½	4½	1½	1	9	1½	3 = 276	Total
Oligochaeta																						
Lumbriculidae		3			2	5					6	2			1		1					20
Naididae																						
Nais cf. *barbata* Muller			1																			1
Paranais litoralis (Muller)			3																			3
Pristina Ehrenberg				1																		1
Slavina appendiculata (d'Udekem)			2																			2
Tubificidae																						
Ilyodrilus templetoni (Southern)			1																			1
Limnodrilus claparedianus Ratzel						5		1											5			11
L. hoffmeisteri Claparede						18					1	4					4		15	2	1	45
Rhyacodrilus montanus (Brinkhurst)						6																6
Immature with capilliform chaetae		1	1		2	13		1	1	1		1	1									22
Immature w/o capilliform chaetae		2		4	2	85		5			9	2	1	3	1		4		12	1	3	124
																						236
Insecta																						
Chironomidae																						
Tanypodinae																						
Macropelopini																						
Procladius Skuse	13	17	4	32	11	129		10	5	3	6	39	48	2	1	3	41		34		1	400
Diamesinae																						
Diamesini																						
Potthastia (Kieff.)		1																				1
Protanypini																						
Protanypus hamiltoni Saeth.				7	10	23		1			9	10					8		3	2		73
Prodiamesini																						
Monodiamesa prolibata Saeth.		1		1	1	4																7
Orthocladiinae																						
Cricotopus (v.d. Wulp)						1																1
Heterotrissocladius latilaminus Saeth.		5			1	3																9
Heterotrissocladius oliveri Saeth.				5		18		2	1	2	13	10	5				4		3			63
Paracladius cf. *alpicola* (Zett.)		3																				3
Parakiefferiella (Thien.)	13				7	3	1						1									25
Psectrocladius (Kieff.)	2					4																6
Chironomini																						
Chironomus (Mieg.)			3		2	27					12	4			3	3	6		27	3	3	93
Cladopelma Kieff.						1																1
Cryptochironomus Kieff.		1			1																	2
Demicryptochironomus Lenz		1																				1
Dicrotendipes Kieff.					1																	1
Microchironomus Kieff.	3																					3
Microtendipes Kieff.		1																				1
Pagastiella Brund.	33																					33
Paracladopelma Harn.	1					1																2
Paralauterborniella Lenz	1	1																				2
Stictochironomus Kieff.		1		87	39	267	1	13	6	2	52	104	46	20	20	1	26		200	2	2	889
Tanytarsini																						
Cladotanytarsus Kieff.	13	2			2																	17
Micropsectra Kieff.				3		5				1					2	1						12
Tanytarsus v.d. Wulp		18	1	2	3	3					1	1	1									29
Zavrelia Kieff.					1	2																3
																						1,677

Chironomus in this study, tentative separations of those larvae yielded about 95 percent *C. atritibia* type and only 5 percent *C. attenuatus* type. No larvae of the *C. semireductus* Lenz or *C. plumosus* (L) types were noted.

Saether (1970) and Saether and McLean (1972) did not use a holistic approach in their typing of British Columbia lakes utilizing chironomid distributional data. Instead they demonstrated that different areas of the same lake can have vastly different typologies. They reported that the presence of *Heterotrissocladius subpilosus* type larvae was indicative of ultraoligotrophic conditions, *Stictochironomus* illustrates a moderately oligotrophic to mesotrophic situation, and the presence of *Chironomus plumosus* and *C. semireductus* types suggests a strongly eutrophic situation.

TABLE 3. Depth distribution of all aquatic macroinvertebrates collected in Flathead Lake.

Taxa	Depth (m)
Hydrazoa	16-18
Turbellaria	16-29
Nematoda	9-47
Bryozoa	9-37
Oligochaeta	9-55
Lumbriculidae	9-55
Tubificidae	9-55
Amphipoda[1]	4-29
Ephemeroptera[2]	4-33.5
Trichoptera[3]	4-18
Hydracarina	4-27
Diptera-Chironomidae	4-55
Mollusca	6-47
Gastropoda[4]	6-37
Pelecypoda[5]	6-47

[1]—*Hyalella azteca*
[2]—*Caenis, Ephemera*
[3]—*Molanna*
[4]—*Gyraulus, Physa, Lymnaea*
[5]—*Pisidium, Muscilium*

The dominant chironomids in Flathead Lake differed considerably from those of Lake Sammamish, Lake Washington, or any of the Okanagan Valley Lakes. Unfortunately, the most abundant genera collected in Flathead Lake, *Stictochironomus* and *Procladius,* were not identified to species because of the lack of adult specimens. Probable species designations for these two genera can only be inferred from published distributional records.

Saether (1975) noted there are eleven described species of *Stictochironomus* in North America and two to three of these are probably profundal inhabitats. *S. rosenscholdi* Zett. is characteristic of median oligotrophic and mesotrophic lakes and is present in nearby British Columbia, as is the shallow water form *S. histrio* Fabr. (Saether and McLean 1972). Sublette and Sublette (1965) recorded *S. virgatus* from Montana.

Roback (1971) noted that *Procladius* larvae are predators that feed on other chironomids and small crustaca. *P. (Psilotanypus) bellus* (Loew) is known from Montana and *P. (Procladius) freemani* Sublette has been previously collected on the west shore of Flathead Lake (Roback, 1971). Other species known in this general area of

North America include *P. (Ps.) nietus* Roback, *P. (P.) ruris* Roback, *P. (P.) abetus* Roback, and *P. (P.) denticulatus* Sublette.

Chironomus anthracinus Zett. is known from Montana (Curry, 1962), and this species may include the *C. attenuatus* type larvae that Saether (1972) collected in moderately eutrophic lakes of British Columbia. *C. atritibia* (Malloch) occurs in British Columbia (Curry, 1962), and this species may be identical to the *C. salinarius* type of cold-stenotherm collected in British Columbia by Saether and McLean (1972). The absence of *C. plumosus* and *C. semireductus* types in Flathead Lake suggests that areas of serious enrichment were not encountered.

The Oligochaeta fauna of Okanagan Lake are similar to the fauna of Flathead Lake (Saether, 1970; Saether and McLean, 1972). However, most of the oligochaete fauna of Flathead Lake is widespread and common in all kinds of freshwater biotopes except *Rhyacodrilus montanus*, which is indicative of a cold, oligotrophic habitat.

Typology of Flathead Lake

Protanypus hamiltoni occurs in three large, deep oligotrophic lakes in British Columbia and on the shore of Great Slave Lake in the Northwest Territory. This species is usually confined to the littoral zone but occurs as deep as 117 m (Saether, 1975a). Since all *Protanypus* species seem to be characteristic of ultraoligotrophic to moderately oligotrophic conditions, its presence at several depths and locations indicates that these conditions exist in most parts of Flathead Lake.

Heterotrissocladius has been found in the littoral to upper profundal zone of lakes and is present in a similar habitat (9 to 21 m) in Flathead Lake. *H. oliveri,* which occurs in the deeper parts of the profundal zone of temperate lakes (Saether, 1975b), was collected from 17 to 37 m depth in Flathead Lake. All species of *Heterotrissocladius* seem to be characteristic of ultraoligotrophic to moderately oligotrophic lakes (Saether, 1975b).

Monodiamesa prolibata is distributed from 9 to 21 m depth and this profundal species indicates oligo-to-mesotrophic nearctic lakes (Saether, 1973, 1975c). If the *Paracladius* cf. *alpicola* identification from Flathead Lake is accurate, it too would be indicative of ultra-to-moderately oligotrophic conditions.

The Oligochaeta and Chironomidae data from Flathead Lake suggest that areas of the lake vary from ultraoligotrophic to mesotrophic. After an anaysis of the algal flora, Gaufin *et al.* (1976) concluded that the lake has oligotrophic characteristics. Water quality and nutrient investigations suggest some shallow bays such as Yellow Bay, Hell Roaring Bay, and Polson Bay are gradually undergoing eutrophication. Potter and Stanford (1975) concluded that Flathead Lake is maintaining its oligotrophic nature as a result of a balance between increased nutrient loading and sedimentation. Analysis of the benthic macroinvertebrate community supports the contention of widespread oligotrophic conditions with areas of ultraoligotrophic and mesotrophic conditions.

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Literature Cited

Brundin, L. 1949. Chironomiden and endere Bodentiere de Sudschweden Urgebirsseen. Rep. Inst. Freshwat. Res. Drottningholm 30:1-914.

Curry, L. L. 1962. A study of the ecology and taxonomy of freshwater midges (Diptera:Tendipedidae) of Michigan with special reference to their role in the "turnover" of radioactive substances in the hydrosol. A. E. C. Prog. Rpt. 149 pp.

Fast, A. W. 1968. A drag dredge. Prog. Fish-Cult. Jan.:57-61.

Gaufin, A. R., G. W. Prescott, and J. F. Tibbs. 1976. Limnological Studies of Flathead Lake, Montana: A Status Report. U.S. Environ. Protection Agency, EPA-600/3-76-039, 84 pp.

Potter, D. S., and J. A. Stanford. 1975. Influences on the plankton communities of oligotrophic Flathead Lake. Verh. Internat. Verein. Limnol. 19:1790-1797.

Roback, S. S. 1971. The Subfamily Tanypodinae in North America. Monogr. Acad. Nat. Sci., Phil. 17:1-410.

Saether, O. A. 1970. A Survey of the Bottom Fauna in Lakes of the Okanagan Valley, British Columbia. Fish. Res. Bd. Canada, Tech. Rept. 196:1-17.

————. 1973. Taxonomy and ecology of three new species of *Monodiamesa* Kieffer, with keys to nearctic and palaearctic species of the genus (Diptera:Chironomidae). J. Fish. Res. Bd. Canada 30:665-679.

————. 1975a. Two New Species of *Protanypus* Kieffer, with Keys to Nearctic and Palaearctic Species of the Genus (Diptera: Chironomidae). Bull. Fish. Res. Bd. Canada, 193:1-63.

————. 1975b. Nearctic and palaearctic *Heterotrissocladius* (Diptera:Chironomidae). Bull. Fish. Res. Bd. Canada, 193:1-63.

————. 1975c. Nearctic chironomids as indicators of lake typology. Verh. Internat. Verein. Limno. 19:3127-3133.

————, and M. P. McLean. 1972. A Survey of the Bottom Fauna in Wood, Kalamalka and Skaha Lakes in the Okanagan Valley, British Columbia. Fish. Res. Bd. Canada, Tech. Rpt. 342:1-20.

Sublette, J. E., and M. S. Sublette. 1965. Family Chironomidae in Catalogue of the Diptera of America North of Mexico. Agricul. Handbook USDA 276:142-181.

Thut, R. 1965. A Study of the Profundal Bottom Fauna of Lake Washington. Univ. of Washington, Seattle, M.C. thesis. 79 pp.

Townes, H. K. 1945. The nearctic species of Tendipedini (Diptera, Tendipedidae (=Chironomidae)). Am. Midl. Nat. 34:1-206.

Young, R. T. 1935. The life of Flathead Lake, Montana. Ecol. Monogr. 5:93-163.

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Limnological Investigation of Eutrophic Medical Lake, Washington

Abstract

Medical Lake, Spokane Co., Washington, developed ammonia nitrogen and orthophosphate maxima in the hypolimnion following thermal stratification and a large cyanophycean bloom. Phytoplankton decomposition resulted in hypolimnetic oxygen depletion in 69 percent of the lake volume at the height of stratification. High pH values, elevated ammonia nitrogen concentrations, and low dissolved oxygen levels existed throughout the water column following fall overturn.

Rehabilitation of Medical Lake as a productive fishery probably will require nutrient inactivation in conjunction with hypolimnetic aeration to eliminate undesirable environmental conditions.

Introduction

During 1957 the State of Washington Department of Game attempted to rehabilitate Medical and West Medical Lakes (Spokane County) by application of toxaphene and subsequent restocking with *Salmo gairdneri* Richardson. The rehabilitation procedure was not successful at Medical Lake, but worked so well at West Medical that today the lake supports one of the most productive sports fisheries in Eastern Washington (Simons, pers. comm.).

In an effort to determine why two sister lakes both so close to each other and both having apparently similar potentials could react to treatment in such disparate ways, an investigation of Medical Lake was undertaken. The aim of the study was to relate primary and secondary production to the physical and chemical environment, and to determine why the establishment of a large population of fish has been unsuccessful. Of particular interest is the fact that West Medical Lake receives approximately one million gallons (3785.4 m^3) of secondary treated sewage daily from the nearby state hospitals. Also, until 1964 the town of Medical Lake had no municipal sewage treatment system, relying instead on a matrix of cesspools and septic tanks with the concomitant possibility of considerable seepage into Medical Lake.

Description of the Study Area

Medical Lake is a closed basin located approximately 25 km southwest of Spokane, Washington. It has a surface area of 0.61 x $10^6 m^2$, a volume of 6.07 x $10^6 m^3$, and a maximum depth of 18 m. A single sampling station was established at the point of maximum depth.

Methods and Materials

Water samples and field measurements were taken monthly from May to November,

1974. A one-liter Kemmerer sampler was used to collect samples at two meter intervals from the surface to the bottom.

Water Chemistry, Temperature, and Conductivity

Dissolved oxygen (± 2% of the reading), temperature (± 0.2° C), conductivity (± 3% of the reading) and pH (± 0.1 pH unit) measurements were performed *in situ* utilizing a Hydrolab® Surveyor (Model 6). Carbonate and bicarbonate (potentiometer titration), sulfate (turbidimetric method), chloride (mercuric nitrate titration), calcium (EDTA titration), magnesium (calculation), sodium and potassium (flame emission), nitrate (cadmium reduction), nitrite (diazotization), ammonia (nesselerization), orthophosphate (stannous chloride), silica (molybdosilicate), and turbidity (nephelometric method) determinations were made in the laboratory as described by the American Public Health Association (1971).

Light

In situ light intensities were obtained with a Kahlsico submarine photometer (Model No. 268WA300). Measurements were taken at one-meter intervals from the surface to the lower limit of the euphotic zone (1 percent of incident light). Water transparency was measured with a 20 cm Secchi disk and mean vertical extinction coefficients were calculated as described by Hutchinson (1957).

Phytoplankton Standing Crop, Chlorophyll, and Primary Productivity

Equal sample volumes were collected at one-meter intervals from the surface to the lower limit of the euphotic zone and composited. A 250 ml sample of the composite was preserved with Lugol's solution and later used to determine cell volumes and counts per unit volume for each taxon. The sedimentation method was utilized (Schwoerbel, 1970).

Chlorophyll *a* extraction was preceded by sonication to disrupt cell walls, followed by filtration (0.45 micron Millipore® filter) of a known volume of the composite. Chlorophyll *a* concentrations (mg/m^3) were determined as described by the American Public Health Association (1971). The method of Ryther and Yentsch (1957) as modified by Martin (1967) was used to estimate primary productivity.

Zooplankton Standing Crop

Bottom to surface oblique tows were made with a Clarke-Bumpus sampler to obtain quantitative zooplankton samples. All zooplankton samples were preserved with formaldehyde and stained with 1.0 ml of saturated eosin Y-ethanol solution and 0.5 ml of Lugol's. A modified rotary counting chamber (Ward, 1955) was utilized to evaluate a minimum of three zooplankton subsamples of 2 ml each.

Results

Light and Temperature

A maximum euphotic zone depth of 6 m occurred on 9 May, while the minimum of 2 m was determined on 2 August. The mean depth for the study was 4.13 m. Signifi-

cant correlations existed between Secchi disk visibility and extinction ($r = -0.73$; $P = 0.05$), and extinction and turbidity ($r = 0.82$; $P = 0.05$). However, the relationship between Secchi disk visibility and turbidity was not significant.

At the initiation of sampling, thermal stratification was evident (Fig. 1). Water below 12 m was 6° C, and surface waters had warmed to 13° C. The height of thermal stratification was detected on 2 August and a well-developed thermocline existed between the four- and six-meter depths. By 22 November, water temperatures had decreased and subsequent mixing initiated fall overturn.

Water Chemistry

Medical Lake is a sodium bicarbonate water and during the study had a mean conductivity of 1687 micromhos/cm, maintaining a pH near 9.4 (Table 1). Mean nitrate and nitrite nitrogen values were 0.37 mg/1 and 0.006 mg/1, respectively.

Dissolved oxygen concentrations of the surface waters on 9 May were near 14.0 mg/1, while the bottom strata had started to become anaerobic (Fig. 1). By 2 August, anoxia existed below the four meter depth. On 22 November, oxygen concentrations in the epilimnion were reduced to 2.0 mg/1 because of mixing with stagnant bottom water.

Orthophosphate concentrations were uniform throughout the entire water column at the onset of sampling (Fig. 2). As the season progressed, the orthophosphate concentrations sharply increased in the hypolimnion and by 18 October concentrations exceeded 2.0 mg/1. At fall overturn, orthophosphate concentrations were reduced to levels near 1.0 mg/1 throughout the entire water column.

Ammonia nitrogen concentrations in the epilimnion were less than 0.5 mg/1 throughout the study, but concentrations in the hypolimnion were greater than 7.0 mg/1 by October, just prior to fall overturn (Fig. 2). Following overturn, concentrations did not exceed 0.40 mg/1.

Phytoplankton Standing Crop

Eighteen species in fifteen genera were identified. The Cyanophyceae comprised 74.41 percent of the total cell volume for the study and were the primary contributors to the standing crop. *Aphanizomenon flos-aquae* (L.) Ralfs was the major species, ranking sixth in abundance (2.50 percent) and contributing an absolute mean cell volume of 8.10 $mm^3/1$. "Abundance" in this instance refers to the frequency with which an organism was encountered expressed as a percentage of the total number of organisms observed. *Microcystis aeruginosa* Kuetz. had an absolute mean cell volume of 2.79 $mm^3/1$ and ranked second in abundance (34.72 percent). *Anabaena flos-aquae* (L.) DeBrebisson occurred in 25 percent of the samples, ranking ninth in absolute mean cell volume (0.08 $mm^3/1$) and eleventh in abundance (0.12 percent). *Anabaena* sp. Bory occurred in 37 percent of the collected samples, ranked fifth in abundance (2.64 percent), and produced an absolute mean cell volume of 0.08 $mm^3/1$.

The Bacillariophyceae were second in total cell volume contribution, comprising 14.65 percent. *Cyclotella* sp. Kutz. contributed an absolute mean cell volume of 1.37 $mm^3/1$ and ranked third in abundance (9.15 percent). *Stephanodiscus* sp. Ehr. ranked fourth in abundance (2.87 percent) and fifth in absolute mean cell volume (0.53

$mm^3/1$). *Nitzschia palea* (Kutz.) W. Smith occurred in 37 percent of the collected samples, ranking seventh in abundance (1.82 percent) and eighth in absolute mean cell volume (0.13 $mm^3/1$). *Coscinodiscus* sp. Ehr. and *Nitzschia* sp. Hass. occurred in 13 percent of the samples but contributed little cell volume.

Cryptomonas ovata Ehr. and *Rhodomonas* sp. Karsten were the two genera of the Cryptophyceae identified and comprised approximately 6 percent of the total cell volume. *Cryptomonas ovata* ranked ninth in abundance (0.30 percent) and fourth in absolute mean cell volume (0.87 $mm^3/1$). *Rhodomonas* sp. was less frequent and accounted for only 0.1 percent of the total cell volume.

Least frequently observed were members of the class Chlorophyceae, comprising only 3.02 percent of the cell volume throughout the study. *Staurastrum* sp. Ehr. was the most prevalent green, occurring in 25 percent of the samples, contributing 0.39 $mm^3/1$ to the absolute mean cell volume.

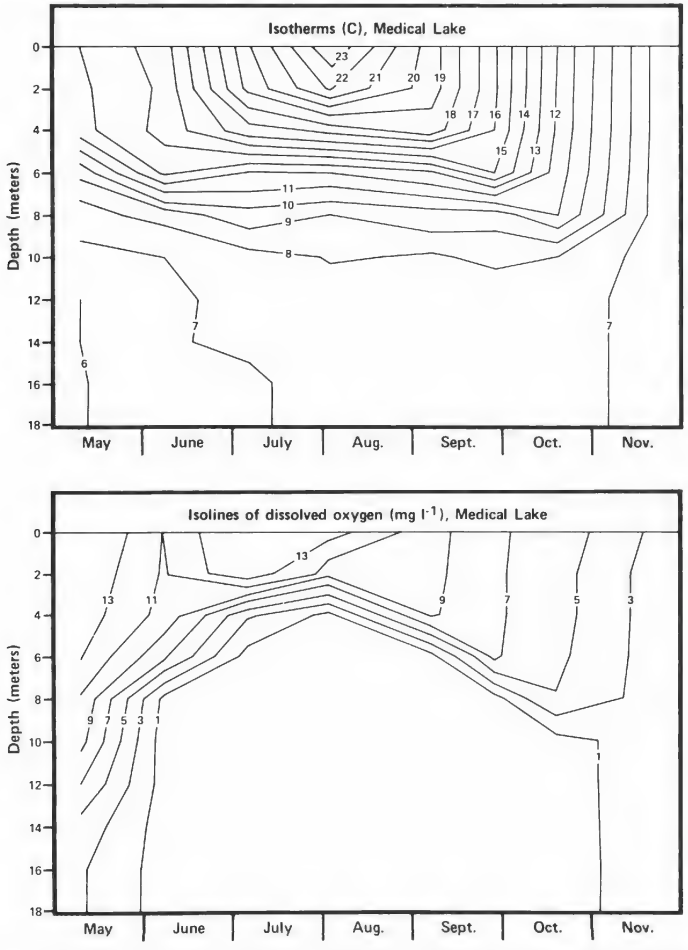

Figure 1. Isolines of temperature and dissolved oxygen, Medical Lake (5/7/74-11/22/74).

Seasonal phytoplankton succession showed that *Cryptomonas ovata* dominated the community in May (Table 2). Maximum cell volumes for *Aphanizomenon flos-aquae* and *Microcystis aeruginosa* occurred in June and August, respectively. *Staurastrum* sp. succeeded the blue-greens in October, but the prevailing algal forms in November were *Cyclotella* sp. and *Stephanodiscus* sp.

The mean daily chlorophyll *a* concentration was 10.10 mg/m^3. The correlation between chlorophyll *a* concentrations and phytoplankton standing crops was not significant.

Mean daily primary production was 0.28 gC/m^2 (0.74 g 0_2). A maximum of 0.50 gC/m^2/day (1.32 g 0_2) was calculated for 2 August. A photosynthetic quotient of unity was used to convert units of carbon to units of oxygen.

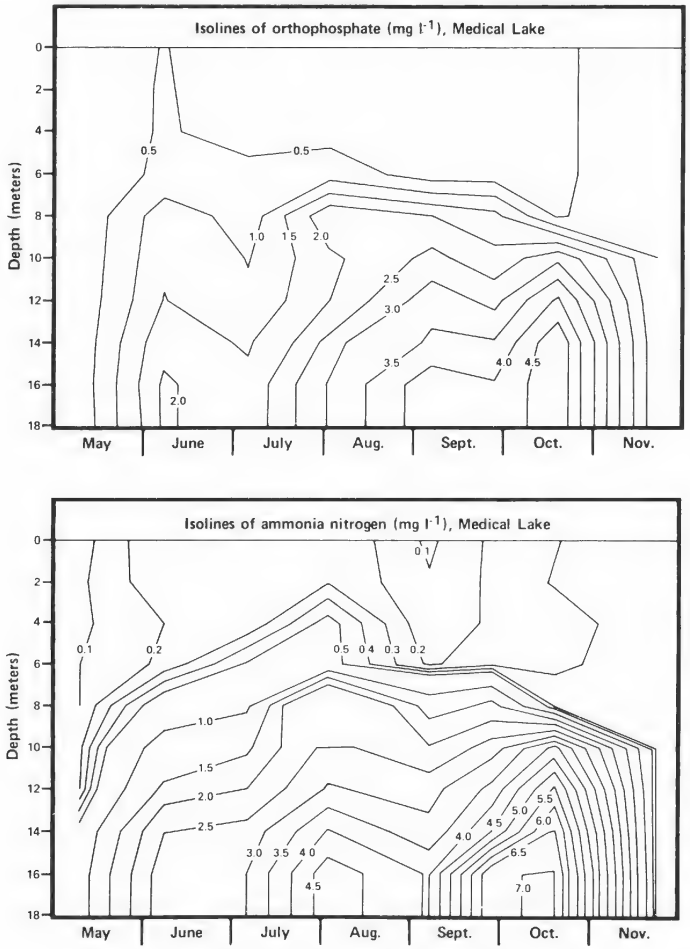

Figure 2. Isolines of orthophosphate and ammonia nitrogen, Medical Lake (5/9/74-11/22/74).

Zooplankton Standing Crop

Eight species in six genera were identified during the study. The Rotifera were most abundant, comprising 84.85 percent of all plankters. The Eucopepoda ranked second, contributing 11.30 percent; the Cladocera accounted for 4.54 percent of the numerical standing crop. The least abundant order was Diptera, which comprised 0.31 percent of the total zooplankton community.

Keratella hiemalis Carlin was the most abundant species, occurring in 75 percent of the samples and comprising 76.41 percent of the numerical standing crop. *Keratella quadrata* Ahlstrom occurred in 25 percent of the samples and accounted for 8.40 percent of the total zooplankton population. *Asplanchna ashlandi* Gossee occurred only in the first collection and contributed little to the standing crop.

The major Eucopepodite, *Diaptomus ashlandi* Marsh, contributed 4.47 percent to the total standing crop and occurred in all collections. *Cyclops bicuspidatus thomasi* S. A. Forbes comprised only 0.39 percent of the standing crop.

The two Cladocera, *Daphnia pulex* (Lidig) Richard and *Daphnia schodleri* Sars, contributed 0.71 and 3.83 percent, respectively, to the total standing crop. *Daphnia pulex* was observed in 75 percent of the samples and *D. schodleri* was present in all collections.

TABLE 1. Range and mean of the determined water quality parameters, Medical Lake (5/9/74-11/22/74).

Temperature (°C)	5.9-23.0 10.5	Mg^{++} (meq/1)	0.88-1.28 1.16
Conductance (micromhos/cm)	1620-1800 1687	$Na^{+}+K^{+}$ (meq/1)	13.89-16.63 14.78
Dissolved Oxygen (mg/1)	0-14.7 4.2	NO_3^-–N (mg/1)	0.037-0.737 0.373
pH Range	7.3-9.7	NO_2^-–N (mg/1)	0.001-0.029 0.006
CO_3 (meq/1)	0.68-2.5 1.51	NH_3–N (mg/1)	0.06-7.05 1.45
HCO_3 (meq/1)	11.52-14.56 13.43	Ortho-$PO_4^{\equiv}$(mg/1)	0.01-4.90 1.3
Cl^- (meq/1)	2.36-3.05 2.82	Silica (mg/1)	2.1-9.1 7.0
SO_4 (meq/1)	0.61-0.76 0.69	Turbidity (N.T.U.)	1.2-5.1 2.8
Ca^{++} (meq/1)	0.90-1.37 1.06		

TABLE 2. Medical Lake algal succession (5/9/74-11/22/74) expressed in mean phytoplankton cell volume ($mm^3/1$).

	May	June	July	Aug.	Sept.	Oct.	Nov.
Cryptomonas ovata	5.20*	0.96			0.26	0.26	
Aphanizomenon floa-aquae		24.75*	19.54	17.42	0.91	1.08	0.22
Microcystis aeruginosa				4.94*	4.69	3.16	
Staurastrum sp.					0.23	2.70*	
Cyclotella sp.	0.46					3.57	6.94*
Stephanodiscus sp.							4.26*

* indicates seasonal maximum

Table 3 shows that both *Daphnia pulex* and *Daphnia schodleri* had reached seasonal maximums in June. The *Chaoborus* sp., which peaked in July, maintained a low density throughout the study. *Keratella quadrata* succeeded *Chaoborus* sp. by August and in September *Cyclops bicuspidatus thomasi* had reached its greatest density. The October collection was dominated by *Keratella hiemalis* and *Diaptomus ashlandi.*

TABLE 3. Medical Lake zooplankton succession (5/9/74-11/22/74) expressed as numbers/1.

	May	June	July	Aug.	Sept.	Oct.	Nov.
Daphnia pulex	3.4	4.5*	0.5	1.0	0.5		0.2
Daphnia schodleri	4.0	16.2*	4.8	14.6	10.8	6.6	
Chaoborus sp.	0.6	0.4	1.2*	1.0	0.5	0.3	0.2
Keratella quadrata				106.2*	6.2		
Cyclops bicuspidatus thomasi				1.3	2.1*		
Diaptomus ashlandi	9.9	10.3	6.6	7.3	7.4	18.7*	
Keratella hiemalis	202.4	73.4	1.4		71.3	623.3*	35.4

* indicates seasonal maximum

Discussion

Medical Lake began to stratify in May and hypolimnetic dissolved oxygen concentrations were low as a state of anoxia began to develop below the thermocline. At the height of stratification, 69 percent of the total lake volume was anaerobic. This condition was primarily the result of decomposition of phytoplankton on the bottom. Intensive respiratory activity was also indicated by the lower hypolimnetic pH values (less than 7.5) during the height of stagnation.

Ammonia nitrogen and soluble orthophosphate maxima in the hypolimnion during the anaerobic period were the result of continued phytoplankton decomposition. The orthophosphate maximum was also attributed to the release of phosphate from the reduced sediments.

At the onset of sampling the phytoplankton were dominated by *Cryptomonas ovata* and *Cyclotella* sp.; however, the Cyanophyceae became abundant as the season progressed. *Aphanizomenon flos-aquae* comprised more than 95 percent of the total cell volume during late spring and early summer. The abrupt decline of other algal species may have been the result of a shading effect caused by the large *Aphanizomenon* standing crops (Martin, 1967; Soltero and Wright, 1975). The majority of the *Aphanizomenon* bloom occurred while temperatures ranged between 19 and 23° C. In September, when temperatures declined, the *Aphanizomenon* cell volumes decreased sharply. Knutson (1970) described a similar relationship between *Aphanizomenon* blooms and temperature for Lake Ashtabula.

Phosphorus, inorganic nitrogen, and silica are often considered limiting to phytoplankton growth when concentrations fall below 0.01, 0.30 and 0.40 to 0.60 mg/1, respectively (Sawyer, 1947 and 1952; Hutchinson, 1967; Macan, 1970). The aforementioned nutrient levels were exceeded at all times and not considered limiting to algal growth.

The effect of zooplankton grazing must be considered when declines in phytoplankton standing crops occur. Many researchers (Anderson, Comita, and Engstrom-Heg,

1955; Comita and Anderson, 1959; Edmondson, Comita, and Anderson, 1962) have found a decline in phytoplankton standing crops resulting from zooplankton grazing. Knutson (1970) showed high densities of *Daphnia* during almost uni-algal blooms of *Aphanizomenon* and concluded that *Daphnia* were grazing on the blue-greens. Significant correlations existed in Medical Lake among Cyanophyceae cell volume and Cladocera density ($r = 0.80$; $P = 0.05$), Cryptophyceae cell volume and Eucopepoda density ($r = 0.74$; $P = 0.05$), and Chlorophyceae cell volume and Rotifera density ($r = 0.97$; $P = 0.01$). The correlations may indicate the grazing preferences of the zooplankton and may partially account for the seasonal fluctuations in phytoplankton cell volumes.

Temperature, as well as the phytoplankton community, may have had a pronounced influence on zooplankton composition. *Keratella quadrata* is considered to be a warm water rotifer while *Keratella heimalis* is a cold water species (Hutchinson, 1967). The temperature effect on the zooplankton community is illustrated by the *K. quadrata* maximum when epilimnion temperatures reached 23° C and the peaks of *K. heimalis* during the spring and fall when water temperatures were much cooler (12-13° C).

The lower summer zooplankton standing crops per unit volume resulted from sampling the anaerobic portion of the water column in conjunction with the oxygenated segment. Oxygen requirements for most zooplankton would have dictated the establishment of the majority of the Medical Lake population in the oxygenated epilimnion.

Medical Lake biological productivity (phytoplankton and zooplankton) would appear capable of supporting a fishery, but current water quality would inhibit its success. Dissolved oxygen concentrations of at least 5 mg/1 are considered desirable for a productive fishery while concentrations less than 3 mg/1 have been considered hazardous or lethal (Anon. 1955; 1956; 1960). Ammonia toxicity has been shown in trout at concentrations of 0.2 to 0.7 mg/1 NH_3 (Mc Kee and Wolf, 1963). Additionally, low dissolved oxygen concentrations (Downing and Merkens, 1955) and elevated pH (Ellis, 1937) have a synergistic influence upon ammonia toxicity. During fall overturn, Medical Lake experienced low dissolved oxygen concentrations, a high pH, and toxic ammonia concentrations throughout the water column. Maintaining a healthy trout population under these conditions appears unlikely.

Also, hydrogen sulfide odor was detected in the hypolimnetic samples during summer stagnation. The potential toxicity associated with the production of hydrogen sulfide indicates an additional hazard to be considered when establishing a fishery (Mc Kee and Wolf, 1963).

The ecology of many waters is currently being altered by aeration. Destratification systems elminate hypolimnetic oxygen depletion, ammonia toxicity, and hydrogen sulfide production while increasing bottom temperatures. However, excessive Cyanophyceae and Chlorophyceae blooms have been stimulated by the circulation of nutrients from the hypolimnion (Haynes, 1974). Fast (1973) suggested the use of hypolimnetic aeration as a replacement for destratification systems. Hypolimnetic aeration eliminates the problems associated with anaerobic decomposition without altering stratification and maintaining sediment integrity, thereby minimizing the ecological impact of the aeration process.

Nutrient inactivation has been utilized in some lakes to eliminate excessive phosphorus concentrations which can cause nuisance algal blooms. Horseshoe Lake, Wis-

consin, was treated with slurried alum, and the result was a reduction of total hypolimnetic phosphorus, elevation of dissolved oxygen concentrations, and elimination of excessive algal blooms (Peterson *et al.,* 1973). Funk *et al.* (1975) treated enriched Liberty Lake, Washington, with slurried alum and effected an 88 percent reduction in total phosphorus. Extensive blue-green algal blooms ceased for the growing season after treatment and the following year when project sampling terminated.

Rehabilitation of Medical Lake will probably require the application of a binding agent such as aluminum sulfate in conjunction with hypolimnetic aeration to eliminate toxic ammonia concentrations, hypolimnetic oxygen depletion, and excessive phosphorus buildup. Such treatment should decrease nuisance algal blooms and maintain a suitable habitat for fish.

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Literature Cited

American Public Health Association. 1971. Standard Methods for the Examination of Water and Wastewater. 13th Ed. A.P.H.A., New York. 874 pp.

Anderson, G. C., G. W. Comita, and V. Engstrom-Heg. 1955. A note on the phytoplankton-zooplankton relationships in two lakes in Washington. Ecology 36:757-759.

Anon. 1955. Aquatic life water quality criteria, first progress report. Ohio River Valley Water Sanitation Commission, Aquatic Life Advisory Committee. Sew. Ind. Wastes J. 27:321-331.

Anon. 1956. Aquatic life water quality criteria, second progress report. Ohio River Valley Water Sanitation Commission. Sew. Ind. Wastes J. 28:678-690.

Anon. 1960. Aquatic life water quality criteria, third progress report. Aquatic Life Advisory Committee of the Ohio River Valley Water Sanitation Commission (ORSANCO). J.W.P.C.F., 1959 32:65-82.

Comita, G. W., and G. C. Anderson. 1959. The seasonal development of a population of *Diaptomus ashlandi* Marsh, and related phytoplankton cycles in Lake Washington. Limnol. Oceanog. 4:37-52.

Downing, K. M., and J. C. Merkins. 1955. The influence of dissolved-oxygen concentration on the toxicity of un-ionized ammonia to rainbow trout (*Salmo gairdneri* Richardson). Ann. Appl. Biol. 43:243-246.

Edmondson, W. T., G. W. Comita, and G. C. Anderson. 1962. Reproductive rate of Copepods in nature and its relation to phytoplankton population. Ecology 43:625-633.

Ellis, M. M. 1937. Detection and measurement of stream pollution (related principally to fish life). U.S. Dept. of Comm. Bur. of Fisheries. Bull. 22.

Fast, A. W. 1973. Restoration of eutrophic lakes by artificial hypolimnetic oxygenation. *In* Human-Excelerated Eutrophication of Fresh-Water Lakes, conference proceedings pp. 21-34. Teatown Lake Reservation, Brooklyn Botanic Garden, Ossining, New York.

Funk, W. H., H. L. Gibbons, D. A. Morency, S. K. Bhagat, G. C. Bailey, J. E. Ongerth, D. Martin, and P. J. Bennett. 1975. Determination, Extent, and Nature of Nonpoint Source Enrichment of Liberty Lake and Possible Treatment. Wash. St. Dept. of Ecology Project No. 22, Project Completion Report. 163 pp.

Haynes, R. C. 1974. Some ecological effects of artificial circulation on a small eutrophic lake with particular emphasis on phytoplankton. II. Kezer Lake experiment, 1959. Hydrobiol., 46:141-170.

Hutchinson, G. E. 1957. A Treatise on Limnology. I. Geography, Physics and Chemistry. John Wiley and Sons, Inc., New York. 1015 pp.

————. 1967. A Treatise on Limnology. II. Introduction to Lake Biology and the Limnoplankton. John Wiley and Sons, Inc., New York. 1115 pp.

Knutson, K. M. 1970. Plankton Ecology of Lake Ashtabula Reservoir, Valley City, North Dakota. North Dakota State University, Fargo, Ph.D. Dissertation. 99 pp.

Macan, T. T. 1970. Biological Studies of the English Lakes. American Elsevier, New York. 260 pp.

Martin, D. B. 1967. Limnology Studies on Hebgen Lake, Montana. Montana State University, Bozeman, Ph.D. Dissertation. 126 pp.

Mc Kee, J. E., and H. W. Wolf (Eds.). 1963. Water Quality Criteria. 2nd Ed., California State Water Quality Control Board, Sacramento. Pub. No. 3-A. 548 pp.

Peterson, J. O., J. P. Wall, T. L. Wirth, and S. M. Born. 1973. Eutrophication Control: Nutrient Inactivation by Chemical Precipitation at Horseshoe Lake, Wisconsin. Wis. Dept. of Nat. Res., Tech. Bull. 62, Madison. 20 pp.
Ryther, J. H., and C. S. Yentsch. 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. Oceanog. 2:281-286.
Schwoerbel, J. 1970. Methods of Hydrobiology (Freshwater Biology). Pergamon Press, New York. 200 pp.
Sawyer, C. N. 1947. Fertilization of lakes by agriculture and urban drainage. J. New England Water Work Assn. 60:109-127.
————. 1952. Some new aspects of phosphates in relation to lake fertilization. Sew. and Ind. Wastes J. 24:768-776.
Simons, Richard. 1973. Personal Communication. Regional Fish Biologist, Washington State Department of Game, Spokane, Washington.
Soltero, R. A., and J. C. Wright. 1975. Primary production studies on a new reservoir: Bighorn Lake-Yellowtail Dam, Montana. Freshwater Biol. 5:407-421.
Ward, J. 1955. A description of a new zooplankton counter. Quart. J. Microscop. Sci. 96:371-373.

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Vegetation on the Stikine Flats, Southeast Alaska

Abstract

The vegetation of Sergief Island, located in the mouth of the Stikine River, Alaska, was investigated and classified into 11 community types. These community types occur in four habitat types: mudflats, tidal marsh, shrub thicket, and coniferous forest. The most extensive community is dominated by *Carex lyngbyei* which occurs throughout most of the marsh. *Eleocharis palustris, Calamagrostis nutkaensis, Alnus rubra, Picea sitchensis,* and *Tsuga heterophylla* each dominate an extensive community type. Vegetation distribution is controlled by a combination of tidal influences and island physiography. Stream currents and tides result in the growth of Sergief Island to the southwest so that the *Eleocharis* mudflat and the *Carex lyngbyei* marsh grow seaward. The *Alnus rubra* thicket is higher than the marsh and is static at the marsh boundary. It is being invaded by *Picea sitchensis* and *Tsuga heterophylla.* Several previously undescribed community types were encountered and are described. These include vegetation dominated by *Eleocharis palustris,* by *Juncus arcticus,* by *Scirpus validus,* and by *Carex mackenziei.* This marsh appears to be representative of extensive tidal areas in southeast Alaska.

Introduction

The marsh vegetation of the entire Pacific Coast of the United States has received considerably less attention than that of the Atlantic Coast (MacDonald and Barbour, 1974). This fact is particularly true for Alaska, where the work of Hanson (1951) in central and western Alaska, Cooper (1931) in Glacier Bay, Johnson *et al.* (1966) in Cold Bay, and Stephens and Billings (1967) in Chichagof Island represent the bulk of ecological descriptions of tidal lands. Eilers (1975) deals with an Oregon salt marsh, but his thorough review of west coast marsh literature confirms the paucity of ecological studies in southeast Alaskan salt marshes.

The review by MacDonald and Barbour (1974) is a summary of Pacific Coast marsh and beach vegetation. They indicate that floristic data and often qualitative ecological data exist for marshes at the following locations: Knik Arm, Anchorage, Kodiak Island, Homer, Glacier Bay, and the Queen Charlotte Islands (B.C.), but there is little ecological information for the region under discussion. Marshes of the Queen Charlottes may be similar to those of the Stikine Flats, but they have not been studied quantitatively. The distribution and phytosociology of southeast Alaska marshes are poorly known and most marsh descriptions, including those of Hanson (1951) and Johnson *et al.* (1966), are qualitative.

Tidal flats of the interior passage of southeast Alaska are unique in several respects. Those, such as Sergief Island, in the mouths of major rivers are subjected to tidal amplitudes in excess of 6 m, strong daily and seasonal salinity fluctuations, and rapid sedimentation from the silt-laden streams. Several plant community types have previously been identified in coastal Alaska. These include vegetation dominated by

Carex lyngbyei (Stephens and Billings, 1967), *Calamagrostis* ssp. (Hanson, 1951), mixed forbs (Eilers, 1975), and others. However, none has been described in the region in question.

In June 1975, we studied the marshlands at the mouth of the Stikine River (Lat. N 56° 35′ 30″, Long. W 132° 25′ 30″), which enters Dry Strait and the Koknut Flats north of Wrangell. In the mouth of this river is Sergief Island (area = 6.7 km^2), the location of our study. Purposes of this study included: determination of the type of vegetation that occurs on Sergief Island, mapping of the vegetation units determined, a survey of the flora, and determination of the direction of any successional trends.

Methods

The Study Site

Sergief Island receives continual buffeting from the river flow, large tidal amplitudes, and severe storms. Winters are mild (mean January temperature is +2°C) and summers are warm (mean July temperature is 14°C). Mean total precipitation is in excess of 2600 mm (Hultén, 1968). The island consists of a rocky highland on the east side, rising to 561 feet (172 m), dunes on the north side, and tidal flats on the remainder. The flats are dissected by small tidal channels. Figure 1 indicates the location of the island in relationship to surrounding geographic features. The mudflats are sufficiently shallow so that at low tide moose easily move from Sergief Island to neighboring Farm Island to the north and to the mainland.

Because of the combination of river and tidal effects, the substrate is in constant motion. Comparisons of 1973 aerial photographs with June 1975 field observations and the 1951 datum topographic map suggest that deposition is occurring on the northeast (upstream) and southwest ends and the erosion is occurring on the northwest and southeast sides. Two thirds of the island is marsh and the remainder is brush, forest, or dunes. The marshland provides transitory habitat for game birds which attract substantial numbers of hunters during the fall migration. There is some impact on the vegetation from trampling.

Field Methods

In order to prepare a vegetation map, 120 plots were established. Plot size was 100 m^2 in the marsh and 200 m^2 in wooded vegetation. For each plot ten 1-m^2 quadrats were distributed in predetermined locations. Within each quadrat, the percent cover and frequency of each species was noted, and the percentage occurrence of a species in the 10 sample quadrats was calculated. The number of shrub and tree stems was determined in wood plots; for trees, stem diameter at 1.5 m was also determined.

Data Analysis

Classification. The contribution of each species to a particular plot was estimated by calculating its prominence value, the sum of relative cover, and relative frequency. For each plot prominence values total 200. The plots were analyzed by an agglomerative clustering method (MDISP) (Orloci, 1967). Goldstein and Grigal (1971) provide details of the algorithm and a program.

Each stand is initially considered a separate group. During each iteration, that

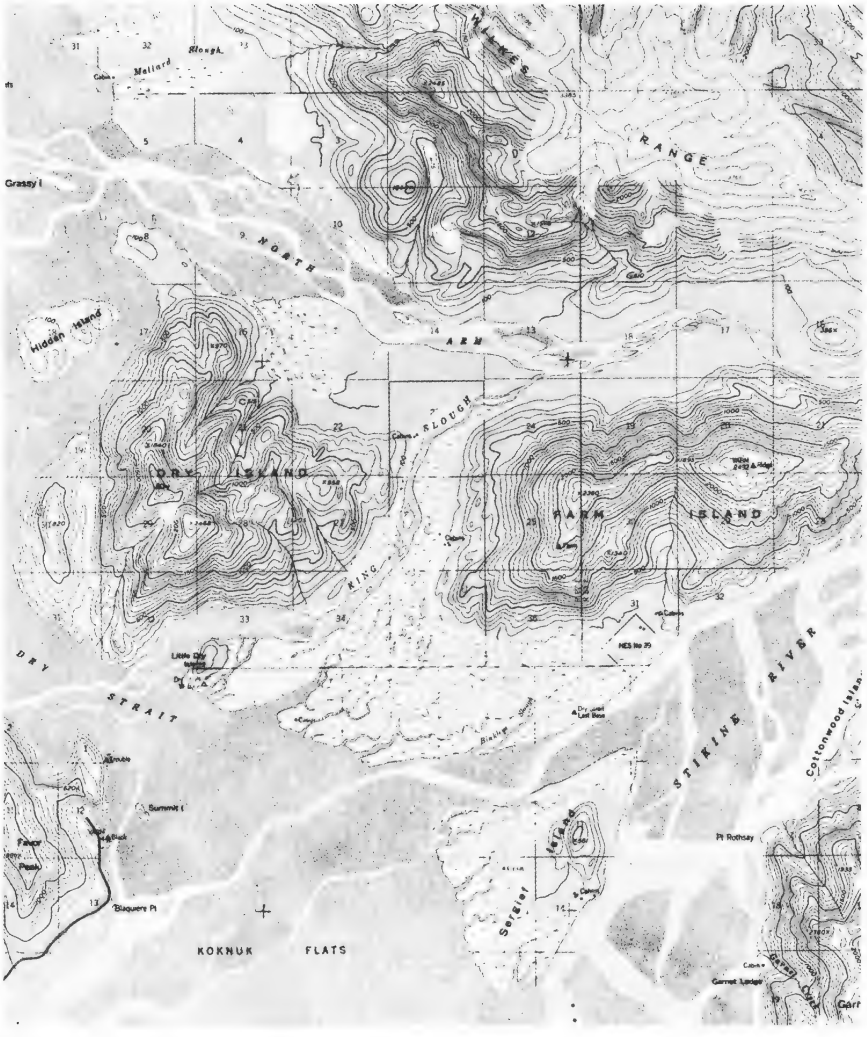

Figure 1. General location of the study area.

pair is joined which results in the least within-group dispersion; that pair becomes a new group and the program continues until all samples are joined. Results of this procedure are summarized by means of a dendrogram which indicates the similarity relationships among every plot. The level at which further merging of samples obscures relationships was determined by inspecting the resulting groups at several levels.

Discrimination. In order to refine the resultant classification and to determine whether any groups should be merged with another, the classification was subjected to stepwise multiple discriminant analysis. This procedure is detailed by del Moral

(1975) and Denton and del Moral (1976) and follows Dixon (1975). Information obtained from this analysis includes a ranking of species in terms of their importance as discriminators, a table of F-values for testing differences between clusters, a classification matrix, the distance of each stand from the mean cluster position, the probability of occurrence of each stand in each cluster, classification functions, an eigenstructure analysis, and the distribution of stands in canonical space. Canonical dimensions result from the discriminant functions by factor analysis such that the canonical axes are mutually independent and each contains more variance than any subsequent one.

The classification was used to produce a vegetation map based on enlarged aerial photographs of the study area. These color photographs were taken in September 1973 and provide considerable detail. Each plot was located on the map and assigned a symbol indicating the community type it represents. Based on a combination of visual evidence and ground truth, the map was constructed at an original scale of 1:5760 (1 km = 17.25 cm).

Taxonomy

We collected specimens of each taxon encountered. Hultén (1968) was the primary nomenclatural authority. However, the taxonomy often disagrees with generally accepted interpretations of taxa extending far to the south. In such cases, we followed Welsh (1974). Herbarium specimens were deposited with the U.S. Forest Service, Juneau, Alaska. A separate publication has been prepared (Sparks, *et al.,* 1977) to detail the flora.

Results and Discussion

Classification

The 120 plots were clustered by MDISP to produce 11 community types and 10 mapable units. The community types join at markedly different similarity levels, a function of greatly different vegetational complexity along a transect from tidal flats to coniferous forests. The dendrogram (Fig. 2) summarizes the relationships between samples. Simple community types, dominated by *Eleocharis palustris* or *Carex lyngbyei,* are joined at very high levels of similarity; the more complex community types have greater within-type variation which results in reduced similarity both within and between community types. The degree of difference required to separate community types meaningfully is not constant throughout the study. It often is constant where the vegetation is more homogeneous. The increased complexity along a transect from tidal flats to forest reflects the reduction of stresses associated with tidal action and salinity.

Discriminant Analysis

Any attempt to classify vegetation obtained from a continuously varying landscape can be enhanced by the use of discriminant analysis. A provisional classification can be improved by objectively reallocating marginal or outlier samples and by determining the statistical validity of previously determined classes. The analysis also suggests a strategy for making a key to the types of vegetation.

The vegetation classes were subjected to discriminant analysis using species as the

discriminant variables. A single sample was shifted from a type dominated by *Calamagrostis* to a closely related one dominated by *Salix barclayi.* In virtually every other instance, the probability of a sample having been correctly classified is 100 percent, demonstrating the excellent segregation obtained using MDISP.

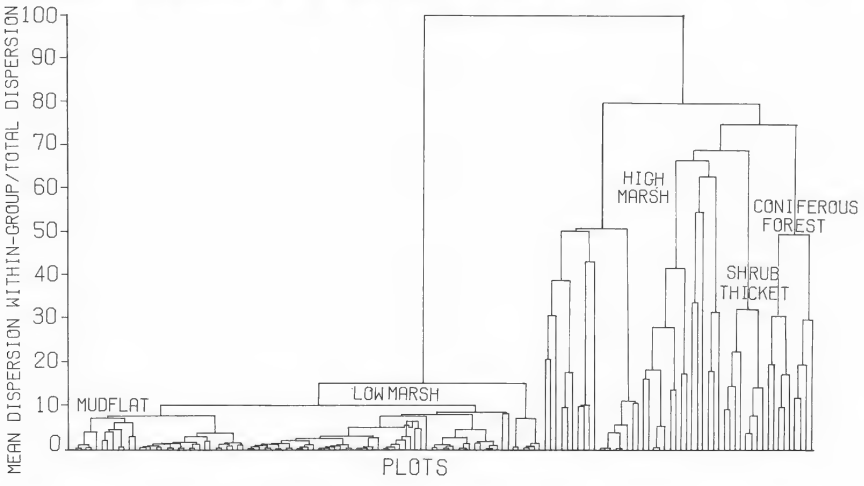

Figure 2. Dendrogram providing the initial classification of plots.

Discriminant analysis has been shown to be a good way to distinguish community types (del Moral, 1975; Grigal and Ohmann, 1975). We have found that optimum discrimination occurs when about 50 percent of the variance occurs in the first discriminant axis. In this case, 46 percent occurs in the first, 18 percent in the second, and 13 percent in the third. The correlations between the original discriminating variables (species) and the canonical axes are 98.1, 95.4, and 93.8 percent, respectively.

Based on species ranked by their discrimination ability, a key to the vegetation types was prepared (Table 1). This key is based on cover data and recognizes five habitat types and eleven communities. Vegetation in the field should be readily allocated to a community type by this key.

Community Descriptions

With one exception, the recognized vegetation types can be recognized from aerial photographs and these are mapped in Figure 3. The *Salix barclayi* community type and the *Calamagrostis nutkaensis* community type are very similar and differ primarily in the presence or absence of *Salix.* We have treated these two communities as a single mapable unit, recognized in the aerial photographs by the presence of *Salix,* within a matrix of *Calamagrostis*-dominated vegetation. The *Potentilla egedii-Festuca rubra* community type is mapped, but also occurs in a narrow, unmapable strip along most tidal channels in the upper marsh.

This vegetation map reasonably represents the ground truth, but its accuracy is compromised by three facts. First, while we treat the data as if they are derived from vegetation consisting of a series of discrete units, such is not always the case. Com-

TABLE 1. Prominence values of common species in eleven community types on the Stikine Delta.

Species	Community Types										
	Eleoc.	Car. Lyg	Pot-Fes	Juncus	Scirpus	Car. Mac	Alnus	Salix	Calamg.	Picea	Tsuga
Achillea borealis Bong.		.1	5.4	9.5		2.0	5.0		7.0	.2	
Alnus rubra Bong.		.1					51.5	.2	.4	10.4	1.6
Angelica genuflexa Nutt.							2.8	2.0	12.7	8.7	
Calamagrostis nutkaensis (Presl.) Steud.		1.0		.7		3.8	20.1	5.0	47.3	5.4	1.0
Carex lyngbyei Hornem.	29.8	99.6	18.0	9.2		21.0	22.6	.8	7.8	.4	
Carex mackenziei Krecz.		1.6	2.9	12.9		73.5		.7	2.3		
Carex macrochaeta C. A. Mey		.2		.7		1.2	12.4		6.3	3.2	
Cicuta douglasii (DC.) Coult. & Rose		5.3	3.1	2.0		.9	1.5		2.0	.4	
Cicaea alpina subsp. pacifica M. E. Jones		.6					3.8		.2	10.5	13.3
Cornus stolonifera Michx.							1.2			1.6	
Cystopteris fragilis subsp. dickieana [R. Sim] Hyl.										5.2	18.8
Dodecatheon pulchullum subsp. superbum (Pennell & Stair) Hultén		.5	6.4	8.2		4.9		3.4	2.7		12.3
Dryopteris dilatata subsp. americana (Fisch.) Hultén									1.9	12.7	11.5
Eleocharis palustris L. Roem. & Schult.	134.4	28.0	.8	.6					.1		
Elymus arenarius subsp. mollis (Trin.) Hultén		.1	3.2			1.1					
Equisetum arvense var. boreale (Bong.) A. Love		.1	7.8	2.6			7.1	25.1	3.0	15.2	5.6
Festuca rubra L.		.6	21.0	6.1		3.5			3.6		
Glaux maritima L.		4.8	10.3	.3		.5					
Heracleum lanatum Michx.									3.0	1.2	12.7
Juncus arcticus subsp. sitchensis Engelm.		.4	1.5	90.8		2.8		.5	3.5		
Lathyrus maritimus subsp. pubescens Hartm.			3.1					11.0			
Lathyrus palustris subsp. pilosus (Cham.) Hultén		.5	7.3	10.7		10.8		1.1	3.7		
Lysichitum americanum Hultén & St. John							2.8			12.9	
Lysimachia thyrsiflora L.		1.4					7.7	.2	4.4	.7	
Menyanthes trifoliata L.				2.6	8.0		3.4				
Picea sitchensis (Bong.) Carr.							4.6			44.4	7.4

Poa eminens Presl.		2.5	16.2	7.9		18.3		.8	4.0		
Poa pratensis L.		.8	6.8					3.0	9.8		
Populus trichocarpa T. & G.								21.9			
Potamogeton filiformis Pers.	37.9	1.1									
Potentilla egedii subsp. grandis (T. & G.) Hara.		21.6	39.0	15.3		29.8		2.8	6.6		
Potentilla palustris (L). Scop.		.8					17.0	.9	2.4	.6	
Ranunculus cymbalaria Pursh.		9.4	11.7	2.2		6.5	.4		.2		
Salix barclayi var. angustifolia Anderss.		.1	.4					44.3		1.1	
Salix sitchensis Sanson in Bong.								13.7			
Scirpus validus Vahl.					190.0						
Streptopus amplexifolius var. americanus Schult.										9.6	15.7
Trientalis europaea L.		.3		1.7		1.2	5.3	1.3	9.0	2.7	1.1
Triglochin maritim L.		9.0	10.8	3.4		13.4		.1	.3		
Tsuga heterophylla (Raf.) Sarg.											31.2

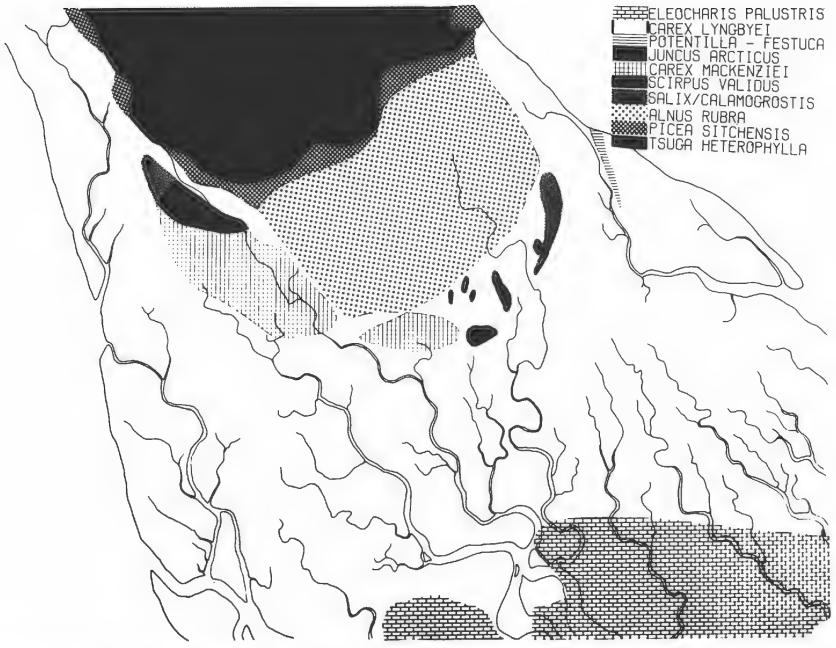

Figure 3. Vegetation map of the southwestern three-fourths of Sergief Island.

munities in the lower marsh often grade imperceptibly into one another and the lines drawn on the map can be arbitrary. Second, because of the constraints of time, logistics, and safety, the sampling intensity was not ideal. Third, while we are confident of the classification and of the key for its interpretation, detailed ground surveys of plot location and elevation were beyond the scope of this study. These limitations result in a map accurate only to about 15 m on the ground or 0.25 cm on the original scale.

The composition of the community types is detailed in Table 2, using the mean prominence value, an index that gives considerable weight to common species. Sporadic and rare species are omitted from this table; their distribution is detailed by Sparks *et al.* (1977).

The *Eleocharis palustris* community type is a sparsely vegetated zone in the lowest marsh areas where tidal action is strongest and salinity greatest. This type does not appear to have been recognized by other workers. Frohne (1953) recognizes a *Carex lyngbyei-Eleocharis palustris* zone in brackish water while others find that various species dominate their most saline habitats. Stephens and Billings (1967) find *C. lyngbyei* in their most saline site; Calder and Taylor (1968) note salt pools dominated by either *Ruppia maritima* or *Zostera maritima;* Hanson (1951) finds either *Puccinellia-Salicornia* or *Triglochin maritima-Potentilla pacifica* dominant in estuaries to the north. We believe that this community type, which includes about 10 percent each of *Carex lyngbyei* and *Potamogeton filiformis,* is typical of unstable, extremely low estuary marshes, but its areal extent is presently unknown.

The *Carex lyngbyei* community type is the most extensive of the study area. It is dominated by *Carex lyngbyei.* Despite the exceedingly large sample (81 plots), it is always the most abundant species. Associated species include *Eleocharis palustris* (28.0) in some lower transitional plots and *Potentilla egedii* (21.6) in other plots. Most of the other species are infrequent or sporadic in upper marsh plots. Some plots contain only *Carex* and many have only one or two more species. This type has been recognized by several other workers, including Stephens and Billings (1967), Frohne (1953), Calder and Taylor (1968), and Keefe (1972). It is generally agreed that this community type is found in brackish rather than truly saline marshes, and its occurrence here speaks for the strong influence of the Stikine River.

TABLE 2. Analytical key to the vegetation types of the Stikine Flats. Values are estimated cover percentages within 100 m^2 plots.

Vegetation dominated by conifers	
Picea sitchensis exceeds 10%, *Tsuga heterophylla* absent	*Picea sitchensis* community
Tsuga heterophylla exceeds 20%	*Tsuga heterophylla* community
Conifers lacking or rare; never dominant	
Aspect dominated by woody species	
Salix barclayi exceeds 10%, *Alnus rubra* absent (mapped with *Calamagrostis* community)	*Salix barclayi* community
Alnus rubra exceeds 25%	*Alnus rubra* community
Aspect dominated by herbs	
True grasses common to abundant	
Potentilla egedii exceeds 10%, *Festuca rubra* common	*Potentilla-Festuca* community
Calamagrostis nutkaensis exceeds 10% (mapped with *Salix* community)	*Calamagrostis nutkaensis* community
Dominance concentrated in Juncaceae (rushes) or Cyperaceae (sedges)	
Juncus arcticus exceeds 30%	*Juncus arcticus* community
Juncus rare; dominance by Cyperaceae	
Scirpus validus exceeds 50%	*Scirpus validus* community
Scirpus validus rare or absent	
Dominance by species of *Carex*	
Carex mackenziei exceeds 10%, usually 30%; high marsh.	*Carex mackenziei* community
Carex lyngbyei exceeds 20%; low marsh.	*Carex lyngbyei* community
Eleocharis palustris dominant, cover exceeds 30%; mudflats	*Eleocharis palustris* community

The *Juncus arcticus* community type is sporadic within the *Carex* marsh. It is fairly rich in species but most are uncommon. After *Juncus* (90.8), the more common include *Potentilla pacifica* (15.3) and *Carex mackenziei* (12.9). This type appears to be associated with local depressions of less brackish water within the low marsh. No mention of a *Juncus* type is found in the salt marsh literature. This community may be local or it may reflect fresh water conditions not mentioned in the literature surveyed.

The *Potentilla egedii-Festuca rubra* community type is scattered throughout the higher marsh areas on Sergief Island and grades into other mixed forb types. It is heterogeneous, poorly defined, and complex. Dominance is shared by *Potentilla egedii* (39.0) and *Festuca rubra* (21.0). *Carex lyngbyei* (18.0), *Poa eminens* (16.2), and many forbs are common. Often this type is found as a matrix for woody species such

as *Populus trichocarpa.* Hanson (1951) mentions several forb communities similar to this one.

The *Carex mackenziei* community type is the more extensive of the three community types recognized within the high marsh zone. Dominance is less pronounced in this zone than the low marsh because vegetational complexity is greater. In addition to *C. mackenziei* (73.5), *Potentilla egedii* (29.8), *Carex lyngbyei* (21.0), *Poa eminens* (13.8), and *Triglochin maritimum* (13.4) are important components of this graminoid-dominated community type. Salinity of this type is lower than that of the low marsh because of reduced tidal inundation. No comparable type appears to have been described in the literature, though it bears floristic relationships to the *Carex ramenskii-Triglochin maritimum-Potentilla maritima* community type identified by Hanson (1951) for brackish to fresher water marshes. It may be a local variant of graminoid-dominated high marsh community types discussed by Stephens and Billings (1967) and Calder and Taylor (1968).

The *Calamagrostis nutkaensis* community type occurs in those areas of high marsh lacking sedges and is quite heterogeneous with a variety of graminoids and forbs. *Calamagrostis nutkaensis* (47.3) is the leading dominant, although not in each of the nine samples. Only *Angelica genuflexa* (12.7) and *Heracleum lanatum* (13.0) achieve a prominence greater than 10, but there are many species in the 5 to 10 range. When *Salix barclayi* is intermixed, we recognize a separate community. Calder and Taylor (1968) recognize a heterogeneous high marsh community type dominated by grasses and forbs to which this type is related. Hanson (1951) recognizes a *Calamagrostis-Myrica gale* high marsh and also a grazing type of *Carex cryptocarpa-Calamagrostis* type that may be related to our samples.

The *Scirpus validus* community type was sampled only once in our study, but is easily seen in aerial photographs. It is a very simple fresh water type, strongly dominated by *Scirpus validus* (190), and only an occasional *Menyanthes trifoliata* (8) or *Conioselium chinense* (2) is to be found. Calder and Taylor (1968) report *S. validus* to be one of many species to be expected in low salinity areas, particularly in the mouths of rivers. It has not been reported as the leading dominant of a community type.

The *Salix barclayi* community type is scattered along a few sloughs and channels of the better drained sites. It is more common on adjacent islands. *Salix barclayi* (44.3) and *S. sitchensis* (13.7) are the dominant woody plants. We recognize this type as a distinct community type, representing shrub communities on well-drained soils, but have mapped it with the *Calamagrostis* community type which forms a matrix for the woody species. Among the many components of the *Salix* type are *Equisetum arvense* (25.1), *Populus trichocarpa* (21.9), *Lathyrus maritimus* (11.0), and *Elymus arenarius* (14.9). *Salix* dominated communities are common in wet, well-drained soils of this region.

The *Alnus rubra* community type is comprised of *Alnus rubra* (51.5) and its associates, primarily *Carex lyngbyei* (22.6), *Calamogrostis nutkaensis* (20.0), *Carex macrochaeta* (12.4), and *Potentilla palustris* (17.0). The transition from marsh to alder communities is fairly abrupt and probably marks the maximum extent of high tides on this island. Many authors have noted *Alnus rubra* associations bordering tidal marshes in southeastern Alaska wherever there is fresh water. However, species composition varies considerably (Stephens and Billings, 1967; Calder and Taylor, 1968).

The *Picea sitchensis* community type occurs extensively over the uplands of southeastern Alaska. Here it appears to be seral to *Tsuga heterophylla. Tsuga* is absent from the fringes of the forest, while *Picea* occurs only as scattered individuals within the main portion of the forest. This highly diverse forest type is mesic and is characterized by *Lysichitum americanum* (13.0), *Equisetum arvense* (15.3), *Alnus rubra* (10.4), *Circaea alpina* (10.5), and several ferns.

The *Tsuga heterophylla* community type is also widespread in Alaska and elsewhere. Here it is the climax upland vegetation. It is less diverse than the *Picea* forest and is dominated by mesophytes. Leading dominants include *Cystopteris montana* (18.8), *Streptopus amplexifolius* (15.7), *Aruncus sylvester* (15.1), *Circaea alpina* (13.3), *Heracleum lanatum* (12.7), and *Dodecatheon pulchellum* (12.3).

Potholes

Scattered throughout the marsh are small, shallow depressions called potholes. These potholes, of various sizes and usually elongated in shape, are seldom more than 15 cm deep at low tide. They contain considerable aquatic vegetation throughout, primarily *Potamogeton filiformis* and *Hippuris tetraphylla.* The margins of such ponds are dominated by *Carex lyngbyei.*

The origin of these natural ponds is unclear, but they are clearly dynamic in character. Our observations lead us to believe that they may represent the middle stage of a successional pattern. The marsh is certainly a dynamic system, one major component of which is the network of drainage channels and sloughs. Periodically, siltation, substrate changes, and blockage by drift wood dam small channels. Once the tidal energy that kept the channel open is removed, siltation begins to fill in the channel. Simultaneously, an impoundment is created upstream. We found ponds in many stages of such developmental sequence. It is likely that there is a cyclic process of channel formation, blockage, pond formation, pond siltation, and, eventually, channel reinitiation. Over the years it is likely that the number of ponds and channels remains fairly stable. We observed several elongated ponds exhibiting a typical, gradual transition to *Carex* on the margins. In each case, the seaward end displays positive signs of a former drainage channel, even though there is now no perceptible current. Blockage appears first to expand the width of the channel forming a pond that is slowly recolonized by *Carex.*

Succession

The dynamics of this marsh are of interest. Are the various communities shifting their positions or their areal distributions? In order to interpret the successional patterns, we have relied primarily on limited size class data for woody vegetation, comparisions of earlier maps (1951), photos (1973), and field data (1975).

Transitions between types in the marsh vegetation are usually gradual; the transition from *C. lyngbyei* marsh to *Alnus* scrub is abrupt, and is correlated with a sharp geomorphological shift. *Alnus* occupies land up to 2 m above the marsh that is marked by a line of driftwood. Throughout the *Alnus* thicket, and gradually increasing in size and density away from the marsh, are scattered individuals of *Picea sitchensis.* There is a sharp transition from the alder thicket to *P. sitchensis* forest that is marked by the beginning of the rock that forms the backbone of Sergief Island. The narrow zone

of *P. sitchensis* grades into a zone dominated by *Tsuga heterophylla* at higher elevation. Size measurements for *Picea* range from 5 cm d.b.h. in the marsh thicket to over 75 cm d.b.h. in the *Tsuga*-dominated forest. Size gradually increases between these mean values. *Tsuga* does not invade the alder thicket and is considerably smaller at the margins of its distribution, averaging 35 cm d.b.h. in the first plots in which they are encountered along a transect into the forest. *Tsuga* does not occur in the margins of the coniferous forest and appears younger than Picea where they occur together. Deep in the forest, *Tsuga* average 70 cm d.b.h. and *Picea* is rare. These data suggest a successional replacement of *Picea* by *Tsuga*. Fonda (1974) found a similar replacement associated with river terrace development in the Hoh River Valley, Washington, where replacement occurred on a time scale of from 1 to 5 millenia. This figure suggests that the Sergief Island replacement is a slow process.

The transition between alder and marsh is abrupt and there is no evidence of any appreciable change in the boundary. While geological processes driving succession, such as subsidence or uplift, may occur, the evidence of this transition indicates that succession is very slow.

Within the marsh itself, there is considerable evidence for vegetation change, some of which has already been discussed with respect to potholes. The series of marsh communities other than *C. lyngbyei* indicate fresher water or better drainage than in the low marsh. Such communities may occur in subsidence depressions (e.g., *Scirpus*) that develop in local areas influenced primarily by fresh water runoff rather than tides. Alternatively, other communities (e.g., *Calamagrostis* or *Potentilla-Festuca*) occur where drainage is better and soils are drier and less saline. When siltation results in higher elevations in the marsh, these types expand slowly at the expense of *Carex lyngbyei.*

The *Carex lyngbyei* and the *Eleocharis palustris* community types bear a distinct environmental relationship to each other and to tidal levels. Any successional shift is driven not by autogenic processes but by physiographic processes including siltation, erosion, and subsidence. Comparisons between the 1951 datum topographic map, the 1973 aerial photos, and our 1975 field observations show that Sergief Island is getting longer, principally on the downstream side which includes the *Eleocharis* community. It is also getting narrower, since several channels shown on the map have been intercepted by a receding shoreline and there is substantial evidence for slumping and undercutting by tidal and stream forces. The result is that the *C. lyngbyei* community type is expanding to the southwest.

We may summarize the dynamics of vegetation on Sergief Island as follows. Woody vegetation does not encroach into the marsh, being checked by tidal action at the extreme high tide line. *Picea* appears to be invading the *Alnus* thicket, while itself being invaded by *Tsuga heterophylla.* Substrate patterns control the distribution of marsh species. High marsh communities appear to be advancing slowly as silt accumulates. Similarly, *C. lyngbyei* and *Eleocharis palustris* appear to be advancing into the mudflats for the same reason. Within the low marsh, potholes are quite numerous and appear to be involved in a cyclic process that results in their number remaining approximately constant.

Summary

We have mapped the distribution of the vegetation of Sergief Island, southeast Alaska,

a region with coastal vegetation. We recognize 11 type of vegetation, though the transition between types is often gradual. Vegetation types dominated by *Eleocharis palustris,* by *Juncus arcticus,* by *Scirpus validis,* and by *Carex mackenziei* have not been described previously. Their distribution in this region is not known. The bulk of the marsh is dominated by *Carex lyngbyei.*

Successional patterns above the extreme high tide line appear to be slow and may be controlled by the rate of soil development; a replacement sequence from *Alnus rubra* to *Picea sitchensis* to *Tsuga heterophylla* is described. Successional patterns within the marsh appear to be controlled by patterns of siltation and erosion and by drainage patterns. The marsh appears to be expanding slowly into the Koknuk Flats as sediment accumulates on the island.

Further studies of the dynamics and distribution of vegetation in this region are required to develop a better understanding of the vegetation ecology of the tidelands of this region.

Acknowledgments

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Literature Cited

Calder, J. A., and R. L. Taylor. 1968. Flora of the Queen Charlotte Islands. Research Branch, Canada Dept. Agric. Monogr. No. 4. 659 pp.

Cooper, W. S. 1931. A third expedition to Glacier Bay, Alaska. Ecology 12:61-95.

del Moral, R. 1975. Vegetation clustering by means of ISODATA: revision by multiple discriminant analysis. Vegetatio 29:179-190.

Denton, M. F., and R. del Moral. 1976. Comparisons of multivariate analyses using taxonomic data of *Oxalis.* Can. J. Bot. 54(14):1637-1646.

Dixon, W. J. 1975. B. M. D. Biomedical Computer Programs. Health Sciences Computing Facilities, Dept. Prev. Med. U.C. Los Angeles. 600 pp.

Eilers, H. P. 1975. Plants, Plant Communities, Net Production, and Tidal Levels: The Ecological Biogeography of the Nehalem Salt Marshes, Tillamook County, Oregon. Oregon State University, Ph.D. thesis. 368 pp.

Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. Ecology 55:927-942.

Frohne, W. C. 1953. Mosquito breeding in Alaska salt marshes, with special references to *Aëdes punctodes* Dyar. Mosquito News 13:96-103.

Goldstein, R. A., and D. F. Grigal. 1971. Computer programs for the ordination and classifications of ecosystems. Ecol. Sci. Div. Publ. 417, ORNL-1BP-71-10.

Grigal, D. F., and L. F. Ohmann. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. Ecol. Monogr. 45:389-407.

Hanson, H. C. 1951. Characteristics of some grassland, marsh, and other plant communities in western Alaska. Ecol. Monogr. 21:317-378.

Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, Calif. 1008 pp.

Keefe, C. W. 1972. Marsh production: a summary of the literature. Marine Science 16:163-181.

Johnson, A. W., L. A. Viereck, R. E. Johnson, and H. Melchior. 1966. Vegetation and flora, pp. 277-354, *in* Environment of the Cape Thompson Region, Alaska, N. J. Wilimovsky and J. N. Wolfe (eds.), U.S.A.E.C., Div. Techn. Infor. Washington, D. C. 1250 pp.

MacDonald, K. B., and M. G. Barbour. 1974. Beach and salt marsh vegetation of the North American Pacific Coast, pp. 175-233, *in* Ecology of Halophytes, R. J. Reimold and W. H. Queen (eds.). Academic Press, Inc., New York. 605 pp.

Orlóci, L. 1967. An agglomerative method for the classification of plant communities. J. Ecol. 55:193-206.
Sparks, L. H., R. del Moral, A. F. Watson, and A. R. Kruckeberg. 1977. The distribution of vascular plant species on Sergief Island, Southeast Alaska. Syesis 10:1-9.
Stephens, F. R., and R. F. Billings. 1967. Plant communities of a tide influenced meadow on Chichagof Island, Alaska. Northw. Sci. 41:178-183.
Welsh, S. P. 1974. Anderson's Flora of Alaska. Brigham Young University Press, Provo, Utah. 724 pp.

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Association News

The 51st annual meeting of the Association was held at Washington State University on March 30, 31, and April 1, 1978. There were 300 registered people in attendance and some 200 papers were delivered. A symposium entitled Science Education and Society was well received. It was highlighted by the banquet address "The Role of Basic Science in Our Society" by Dr. George Pimentel, Deputy Director of the National Science Foundation.

1978-1979 Officers Elected

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Research Grants

John Hoak, University of Idaho, $150, research on grizzlies
Virginia Adams, University of Washington, $125, research on insect pollinators
Diane Besand, Washington State University, research on grass taxonomy

The Association voted to increase dues, beginning in 1979, to the following amounts: Regular Members, $10; Student Members, $5; Individual Sustaining Members, $20; and Institutions with less than 3000 students, $20. Other dues will remain unchanged. The Association also approved a Constitutional amendment which reads: "Vacancy of the office of President is filled by advancement of the Vice President. Replacements for vacancies in other offices shall be appointed by the President."

Extra copies of the programs, including the 200 abstracts from the 51st Annual Meeting of the Northwest Scientific Association, are available. These copies are in the Northwest Science cover and can be purchased from the Treasurer for $3 each, postpaid.

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Annual Variation in the Flowering of Agropyron spicatum near Clarkston, Washington

Abstract

Inflorescence production by 18 plants was recorded in each of 10 years. Although there was a strong tendency toward synchronous vitality, this tendency was not relatable to standard temperature and precipitation data.

Introduction

Year-to-year variation in the vitality of plants is a matter of theoretical interest from both its autecological and synecological points of view. It is also of practical importance in seed collection and vegetation management. Any ability to predict good and bad seed years in advance is especially valuable.

The present report summarizes existing knowledge of the vitality of *Agropyron spicatum* Scribn. & Sm. in the Pacific Northwest, and presents new data from 10 yearly observations of the same individuals growing in the Larson Exclosure located a few km west of Clarkston, Washington.

Previous Observations and Experimental Work

Progeny tests have shown that *Agropyron spicatum* includes individuals which are genetically differentiated into caespitose and rhizomatous biotypes (Daubenmire, 1960, 1970), and since these are segregated environmentally they may be considered as ecotypes, or perhaps better as ecotype groups. In eastern Washington and northern Idaho, at least, it is abundantly clear that only caespitose individuals are found toward the drier limits of the species' environmental range; toward the wetter limits, the grass is represented by rhizomatous plants in all but freshly disturbed soils. On an areal basis, the phytomass of sterile tillers far exceeds that of flowering tillers in rhizomatous populations: the reverse is true for caespitose populations. In one community observed over a number of years (compositional details and environmental data reported as Stand 39, p. 93, in Daubenmire, 1970), individual plants flowered rarely, and weakly then, although the species was well represented by caespitose individuals.

Methods

The new observations reported here were made in an essentially climax stand of the *Agropyron spicatum/Poa sandbergii* association (compositional details and environmental data reported as Stand 56, p. 95, in Daubenmire, 1970), which has been completely protected from livestock, starting long before this study began, and had previously been only moderately grazed. *Agropyron spicatum* is the only sizable grass in the community, and it provides most of the community phytomass. Since the habitat

is near the dry limits of the plant's ecological amplitude, all individuals are caespitose.

Twenty plants were selected to represent essentially the full range of basal diameters. Their positions were recorded, average diameters at the soil surface measured, and inflorescence counts started in 1964. Any inflorescence which appeared to be producing one or more fertile spikelets was counted. This procedure was done after the inflorescences were well developed but before any dissemination. Since observations could not be made in 1970, the annual counts covered a calendar span of 11 years.

Results and Discussion

Of the twenty individuals selected at the start of the study, two died and seven suffered a decline in basal diameter during the study (Table 1). The two that died were near the middle of the size range, with initial diameters of 158 and 177 mm. The death of one of these was associated with the establishment of a colony of ants in the soil beside the base of the plant.

TABLE 1. Numbers of inflorescences produced by each plant, arranged by diameter (mm) of plant and fruitfulness of the population as a whole.

Diam. 1964	Year: 1968	1966	1974	1973	1972	1971	1964	1969	1967	1965	Sum	Diam. 1974	Net change
	Number of inflorescences												
70	0	6	3	6	6	9	20	6	0	43	99	45	−
74	0	5	8	7	11	8	11	31	3	8	92	164	+
77	0	1	0	0	2	14	11	1	8	7	44	96	+
78	0	3	11	6	13	5	0	29	11	4	82	132	+
84	0	1	2	3	7	6	10	14	1	4	48	133	+
100	0	0	1	0	0	5	6	1	2	16	31	71	−
111	0	2	6	25	30	32	71	47	6	66	285	82	−
116	0	1	0	0	0	3	0	26	12	19	61	102	−
122	0	17	0	0	11	28	20	58	82	75	291	69	−
125	0	0	1	4	1	4	1	50	5	18	84	157	+
125	0	4	4	10	2	3	36	37	79	102	277	57	−
135	0	8	25	55	39	43	52	33	99	44	398	186	+
142	0	1	8	7	11	8	4	31	21	33	124	164	+
161	0	4	12	32	14	14	30	39	22	56	223	201	+
167	0	0	1	3	3	1	3	8	5	25	49	160	−
177	0	1	8	0	8	3	6	8	3	12	49	195	+
202	0	16	54	32	78	55	68	109	180	236	828	222	+
217	0	13	29	48	11	58	10	54	54	16	293	268	+
Sum	0	83	173	238	247	299	359	582	593	784	3358	—	—

There was a small tendency for the plants that increased in diameter through the study to be more productive than those that decreased, yet there were some high producers (277, 285, 291 inflorescences) in the decreasing class, with low production (44, 48, 49 inflorescences) among those plants that increased in diameter.

Inflorescence production showed a small positive correlation with basal diameters. The least productive plant (only 31 infl. in 10 seasons) had a basal diameter of 100 mm declining to 71 mm; the most productive (828 infl. in the same period) was 202 mm, increasing to 222 mm. On the other hand, the largest individual (217 mm initially becoming 268 mm) produced only 293 inflorescences in the same period.

There is no suggestion that fruitfulness in one year so exhausts food reserves so as to depress fruiting the following year. For example, 359 inflorescences were produced in 1964, a value in excess of the annual average of 336; yet the highest crop observed (784 infl.) occurred the next year. Thus conditions which presumably initiate flowering in a given year are those subsequent to the preceding flowering season.

Since inflorescences became distinguishable in late May and frost damage to them was never observed, there would seem to be no necessity to consider weather subsequent to early May. Nor did the exceptional low temperature in the winter of 1969 have an evident depressing effect on the flowering as observed a few months later. With this evidence of the apparent immunity of development to low temperatures of winter and spring, attention was directed to autumnal weather. This period starts the rainy season, subsequent to normally dry summers, and could act as a determinant of vitality the following spring.

The records of the official weather station at Lewiston, Idaho, appear to be adequately indicative of weather conditions at the exclosure. Attempts were made to correlate inflorescence numbers with mean monthly temperatures, monthly precipitation, and mean monthly water balance for individual months and for consecutive series of months. Environmental Water Balance was evaluated by the formula: EWB = Precipitation in mm/ (Temperature in °C + 10). The only small correlation discovered was that the spring of zero production had the driest autumn (mean EWB for Sept.-Oct.-Nov. = 0.7) and the year of lowest production had the next driest autumn (mean EWB = 0.8).

There is little doubt but that fruitfulness is governed by a complex set of master factors, since all plants showed zero fruitfulness in 1968, and most showed maximum fruitfulness in 1965. However, all attempts to correlate this behavior with standard temperature and precipitation data have failed, leaving us with no basis for prediction. This virtual lack of success may be due to interactions between weather conditions stimulating flower initials and subsequent weather nullifying this stimulus. It might be helpful to know the approximate date when flower initials are laid down. In any event, experimental manipulation of microclimate in the field will probably be necessary to discover the nature of weather control over flowering in this grass.

Literature Cited

Daubenmire, R. 1960. An experimental study of variation in the *Agropyron spicatum-A. inerme* complex. Bot. Gaz. 122:104-108.

———. 1970. Steppe Vegetation of Washington. Wash. Agric. Exp. Sta. Tech. Bull. 62. 131 pp.

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Plant Succession on the Alnus rubra/Rubus spectabilis Habitat Type in Western Oregon

Abstract

A chronosequence on the *Alnus rubra/Rubus spectabilis* habitat type was studied in Western Oregon. Species composition data were analyzed to determine successional changes along this stand-age gradient. Results showed that early stages were characterized by low species diversity but high species richness and were dominated by graminoids and forbs. Later stages were dominated by shrubs and ferns and were characterized by higher species diversity but the same species richness. There was some indication that species diversity was declining in the latest stages of succession.

Introduction

Communities dominated by *Alnus rubra* and *Rubus spectabilis* occur throughout much of the Oregon Coast Range (Corliss and Dyrness, 1965; Meurisse and Youngberg, 1971; and Franklin and Dyrness, 1973). They are commonly accepted as seral communities in a sere leading to a *Tsuga heterophylla* dominated climax (Franklin and Dyrness, 1973). However, along streams this community type occurs on sites from which more tolerant conifers are precluded. Therefore it is recognized as a climax community type in these situations and such land areas are recognized as belonging to the *Alnus rubra/Rubus spectabilis* habitat type. Fifteen stands on this habitat type were selected from those used by Zavitkovski and Stevens (1972). Their stands were both upland *A. rubra/Corylus cornuta* and streamside *A. rubra/R. spectabilis* communities and were used for overstory biomass determinations. Understory composition and biomass data were taken in these 15 stands to determine successional trends on this habitat type. Periodic flooding is characteristic of these habitats and is believed to maintain a disclimax situation.

Study Area

The study area lies in the Coast Range of Oregon between 44°30′ latitude and 123°30′ and 124°00′ longitude and between 46 and 274 meters (159 and 900 feet) elevation within the *Tsuga heterophylla* vegetation zone (Franklin and Dyrness, 1973). All stands were chosen on the alluvial plain of a major stream to ensure relative uniformity of site factors.

The disturbance factors which have created conditions suitable for red alder establishment in this habitat include periodic flooding, logging, and agricultural clearing.

Macroclimate is maritime with moderate temperatures. The January mean minimum is –2°C and the July mean maximum is 24°C. Total precipitation is about 210 cm, of which 40-50 percent comes in December, January, and February and 6 percent or less comes in June, July, and August (USDC, 1960).

Soils under the sampled stands are ultisolic where there is evidence of soil develop-

ment and inceptisolic or even entosolic where depositional processes are more rapid than developmental processes. Soils are similar to the Winchuck and Nehalem series identified and mapped in adjacent Benton County (USDA, 1975). Parent material in the area is derived mostly from Tyee formation fine sandstone (Baldwin, 1964). Soils have a characteristic mull humus layer (Zavitkovski and Stevens, 1972); A and B horizons are poorly developed, especially in the younger stands; C horizons are deep. Soil texture can vary from gravelly, sandy, silty, or clayey. In a few cases drainage appears to be restricted and the water table may come to the surface. Soil saturation due to high water tables and/or periodic flooding is considered to be a strong influence on the species composition in these stands.

Methods

Eighty-seven nearly pure and well-stocked stands of red alder were located in the Coast Range of Oregon (Zavitkovski and Stevens, 1972). From these stands, fifteen were chosen on river-bottom alluvial soils in the Alsea River drainage. They were as evenly distributed as possible between ages two and sixty-four. Minimum size of the stands was determined by the arrangement of the sample plot. Where possible, the largest stand available in each age class was used to minimize the effects of ecotones.

Each of these stands was visited between 1 August and 7 September 1969. A starting point was located near the center of each stand, and from there a random distance and azimuth were generated which located the starting point of the sample plot. The sample plot for crown coverage of the understory was designed after Daubenmire (1959); it consisted of a macroplot 25 x 15 m that included fifty 20 x 50 cm microplots laid out along two 25 m lines which trisect the microplot, with the long axis of the plot on another random azimuth which would keep the entire plot within the stand. Percent crown coverage was ocularly estimated using the cover classes prescribed by Daubenmire (1959). Average percent crown cover and species frequency were computed for each stand and are presented in Table 1. Percent crown closure of the alder overstory was estimated to the nearest five percent for the fully stocked portion of the stand. The percent of full sunlight passing through the canopy was estimated by using Ozalid paper light sensors described by Friend (1961). Five of these were placed in each stand above the level of the understory layers. An additional five were placed throughout the Alsea drainage in open sunlight for measurement of full sunlight.

Results

Species composition changed markedly during the time span represented by the two-to-sixty-four-year-old stands (Figs. 1-4, Table 1). Some of the species were found at nearly all stand ages. Some of these, including *Carex deweyana,* the moss group as a whole, and to some extent *Sambucus racemosa,* showed no trend with time. Others such as *Athyrium filix-femina, Polystichum munitum,* and *Oxalis oregana* are found in most age groups, but their dominance increased with time. However, most species were present in only part of the age-span studied. These were either too scarce to show a trend or they showed a period of peak dominance, usually flanked on both sides by periods of lesser dominance.

Early stands are dominated by grasses and herbs, and the older stands are dominated

TABLE 1. Percent crown cover and frequency of species encountered under a red alder overstory in stands ranging from 2 to 64 years of age.

Age of stand	2	4	9	11	13	16	20	24	25	35	39	40	49	51	64
SPECIES															
Herbs															
Chrysanthemum leucanthemum	+/2														
Mimulus moschatus	1/12														
Epilobium angustifolium	2/18														
Senecio sylvaticus	+/4				6/26										
Galium trifolium		+/2	2/12												
Oxalis oregana	+/2	1/16		+/+	+/4	+/2				2/26	+/8			11/76	
Montia sibirica	+/4	+/4	1/42	2/64	2/48	1/42	1/24		1/18	+/6	+/14			+/4	+/10
Stellaria media		1/12	1/38	5/52	2/22	2/20			2/50	+/8	1/10		1/26		+/10
Digitalis purpurea		2/12	1/10	5/16	8/30	3/20				+/2	1/6				+/2
Prunella vulgaris			1/14	3/30	1/8	2/18	2/14								
Rubus ursinus		1/14	17/99	17/76	16/86	21/80	6/40	10/50	1/4		19/66	3/20	+/2	1/10	
Stachys mexicana		4/28	3/6	+/+	17/84	13/74	6/43	6/40	14/50		6/44	1/6	6/48		3/36
Tolmeia menziesii		1/4			1/6		5/24	6/38	8/52	15/96	1/12	7/70	3/36		3/30
Viola sempervirens				+/4		1/16	+/2			+/2	+/6		+/8	+/2	+/4
Rumex obtusifolius				+/+		+/4	+/2			+/2	+/+	+/+			
Dicentra formosa				+/+					+/2		+/4				+/4
Urtica dioica					2/16	2/12	3/14	26/86		14/70	1/12	17/72	7/48		5/42
Ranunculus orthorhynchus						6/42	9/38	2/24			6/56	1/12			
Oenanthe sarmentosa						+/2		2/14	11/34	1/28					1/8
Petasites speciosa							1/10		1/4	1/4		1/8			
Asarum candatum							1/2								
Geum macrophyllum							+/4								
Osmorhiza chilensis								+/2		+/10	2/16				1/2
Vancouveria hexandra															
Marah oregana											+/4		+/4		
Graminoids															
Juncus effusus	1/18	+/2													
Agrostis tenuis	+/2	1/22	+/+	5/38	3/38	5/46	+/2	+/2		+/6	1/16	+/2			
Holcus lanatus	1/12	+/2	8/86	6/80	3/28	+/2	4/34	2/18	4/38		1/8	1/6	2/12		4/18
Carex deweyana	2/22		2/6	+/6	1/10	4/40	1/10	6/24	2/20	+/4	+/2	+/2			
Elymus glaucus			6/18	+/2	+/2		+/4	5/38	1/6		7/64				+/4

Luzula parviflorus	1/8			+/2				+/4	+/2					+/2
Glyceria elata	+/4			+/4				6/22						
Anthoxanthum odoratum			+/4											+/2
Carex obnupta								+/2		+/2				
Ferns and fern allies														
Pteridium aquilinum		9/42								+/4			1/4	
Equisetum arvense			+/+											+/4
Polystichum munitum	+/12		3/16	4/22		1/4	3/8	1/8		15/18	4/28	37/92	18/56	32/64
Athyrium filix-femina				1/2	+/2		1/6	+/2	4/22	+/+	3/16	2/8	1/4	5/24
Shrubs														
Salix sp.	1/4													
Rubus laciniatus		+/2		2/8										
Ribes lactustre			+/+											
Rosa sp.			+/2											
Holodiscus discolor		+/2	+/+											
Rubus parviflorus	1/10							+/+		+/2	+/6			
Sambucus racemosa			+/4	5/22	1/18	9/22	4/20	1/6	2/14		2/4		11/26	5/16
Rubus spectabilis	1/6		+/2		+/6		+/+	22/56	41/92	14/40	35/84	53/98	37/60	30/76
Acer macrophyllum								1/2				+/+		
Physocarpus malvaceus									1/2					
Acer circinatum									10/18				4/14	
Vaccinium parviflorum							+/+			+/4				
Rhamnus purshiana											+/2			
Conifers														
Pseudotsuga menziesii	+/4	+/+	+/2				+/+							
Thuja plicata			+/+											
Tsuga heterophylla								+/+						

Figure to left of slash is percent crown cover, figure to right is percent frequency; "1" percent crown coverage represents a crown coverage og 0.5-1.0%; "+" to left of slash indicates less than 0.5% crown coverage and a "+" on both sides of slash indicates the species was in the stand but not tallied in the plot.

by shrubs and ferns (Figs. 1-4). Table 1 presents cover and frequency data for these species and shows the trends in dominance. *Holcus lanatus, Stellaria media, Montia sibirica, Digitalis purpurea, Rubus ursinus,* and *Stachys mexicana* are the major early

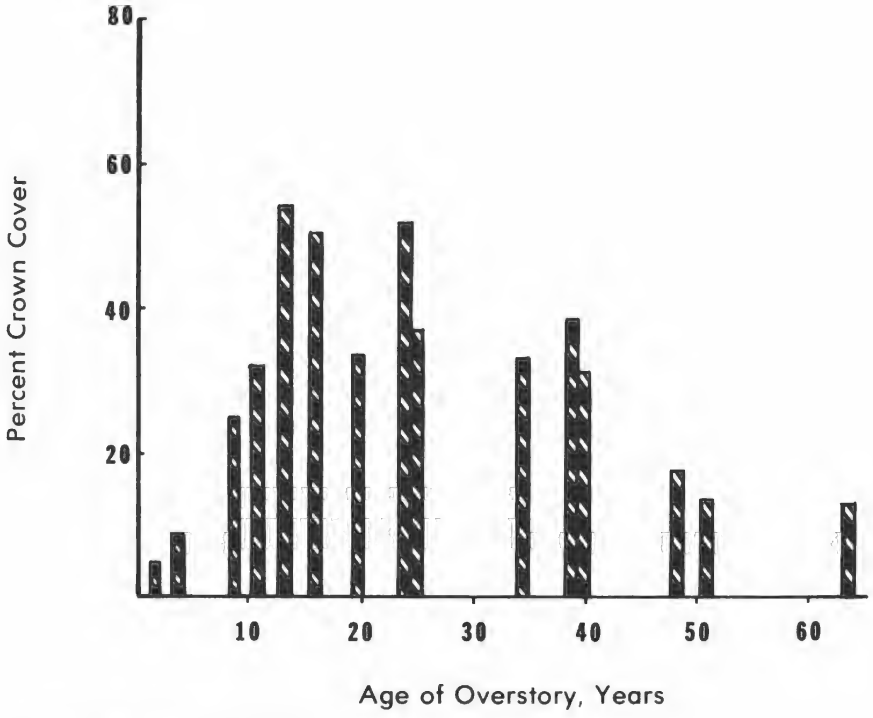

Figure 1. Crown cover of herbaceous species by age of overstory.

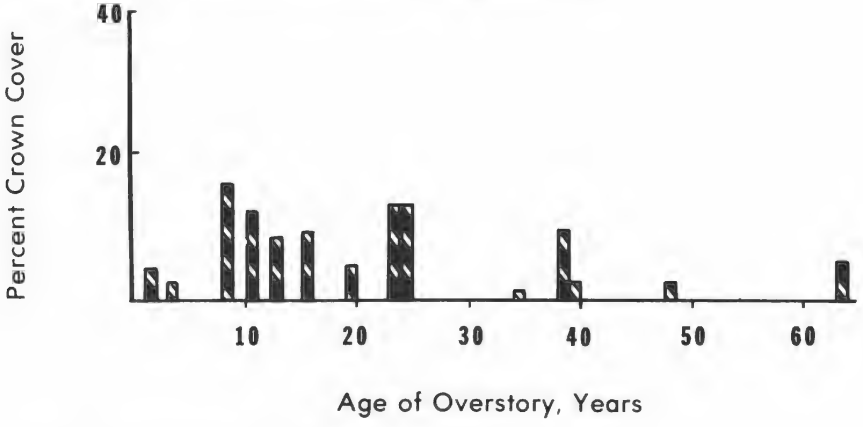

Figure 2. Crown cover of Graminoids by age of overstory.

dominants. *Urtica dioica* and *Tolmeia menziesii* appear as intermediate dominants or transition species between the grass-herb and shrub-fern stages. *Athryium filix-femina, Polystichum munitum,* and *Rubus spectabilis* clearly increase in dominance over time

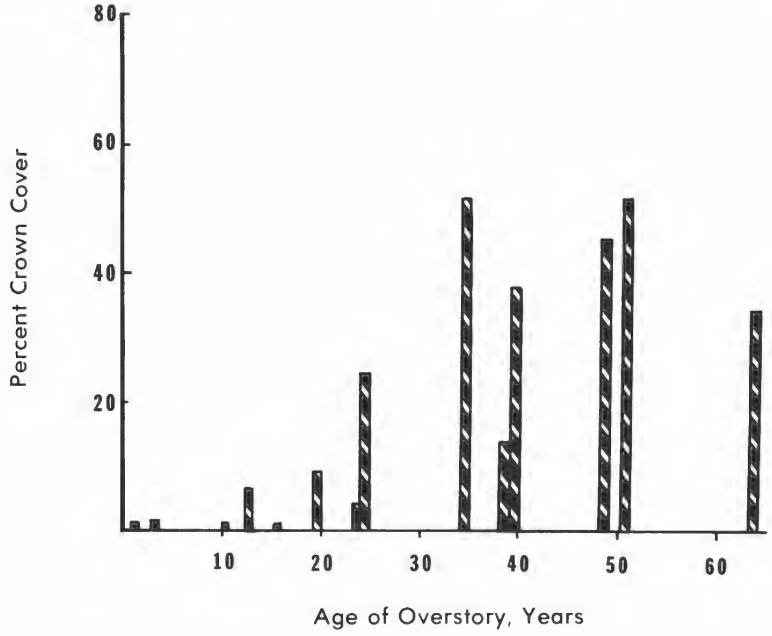

Figure 3. Crown cover of shrubs by age of overstory.

Figure 4. Crown cover of ferns by age of overstory.

in this community and appear to be the only species in a position to assume dominance of the understory in later stages of succession.

Species responses with time were analyzed using linear regression analysis. The trends resulting from these analyses are an unknown combination of autogenic and allogenic processes. Moreover, some of the apparent discrepancies may be due to historical events (floods) which have interceded in the autogenic succession and have set part of the community back to an earlier stage while allowing other parts to proceed.

Total crown coverage for all understory species shows a curvilinear trend reaching about 100 percent crown cover at about age 50 (Fig. 5). This figure is well below the 200 to 300 percent crown coverage found by other authors (Franklin and Pechanec, 1968; Sharpe, 1956) for comparable stands, perhaps because of the different times of data collection. Franklin and Pechanec collected data in early spring, and Sharpe collected in July. This study was made much later in the season, after some of the spring species had disappeared or become rare. Others had declined in vigor, having passed through the flowering and fruiting stages. The data of these two similar studies, therefore, emphasize the crown cover of the early annuals and early herbaceous perennials which contribute very little to the community biomass but may dominate the forest

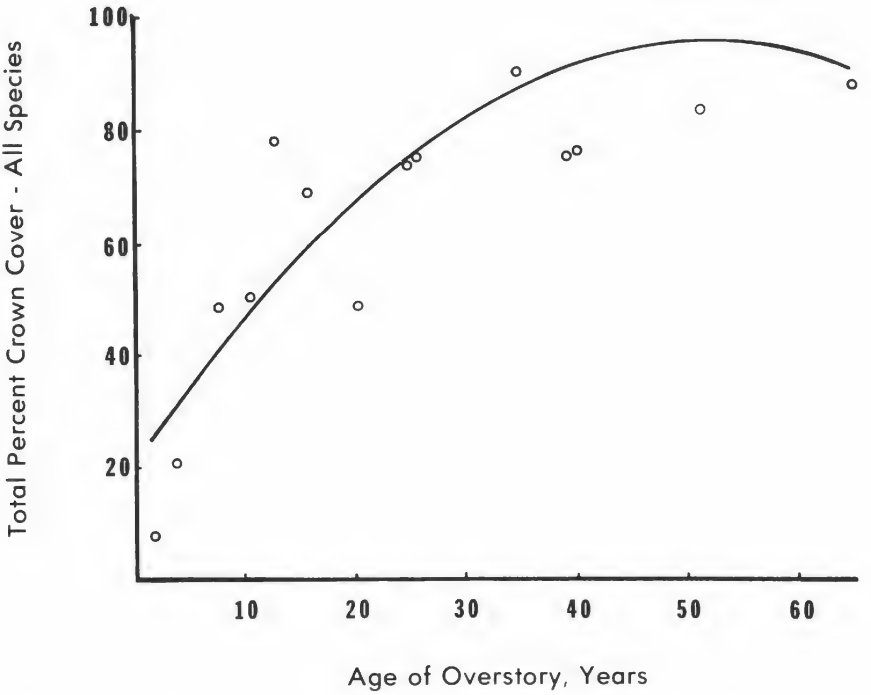

Figure 5. Total crown cover of all species by age of overstory. (Curve fitted by least squares, $y-= 15.6 - 3.3x - 0.034x^2$; $R^2 = .82$. Significant at $\alpha = .05$; $S_e = 15.81$.)

floor layer during certain seasons. Several species, e.g., *Dicentra formosa, Cardamine pulcherrima,* and *Trillium ovatum,* were present or even common in some of the stands visited during a reconnaissance in spring and early summer, but were rare or absent during the data collection period. Some others, like *Montia sibirica* and *Stellaria media,* were noticeably lower in crown cover later in the season.

Odum (1969) and Margalef (1968) have both attributed ecological significance to changes in diversity with succession, while Hurlbert (1971) tried to show that diversity was not an important community attribute.

Changes in species diversity during succession were determined for the 15 stands. The data from the red alder stands fail to show a significant ($\alpha = .05$) trend in total number of species (richness) with time (Fig. 6).

Species diversity was also computed using Brillouin's (1962) index. Brillouin's index uses absolute percent coverage by species and calculates "diversity" by comparing the species coverages in a community with a unit area. Figure 7 shows an initial rapid increase in diversity followed by a flattening of the curve. The possibility of a later decline in species diversity is not precluded by these data. A gradual decline could be expected as the species best adapted to the site replace those less suited, approaching a simpler community with lower species diversity dominated by *Rubus spectabilis* and *Polystichum munitum.*

Conifer reproduction was noticeably scarce in these stands (Table 1). *Pseudotsuga menziesii* seedlings were found in four of the younger stands, but not in any stands over 25 years old. In all cases their ages were the same as that of the alder overstory. Their heights ranged up to one meter.

Only one stand (age 25) had any *Tsuga heterophylla* seedlings. These seedlings were found only on mossy, rotting logs with *Vaccinium parvifolium* and *Polystichum munitum.* The probable source of *T. heterophylla* seed was not located. The high water table in this stand along with the understory competition may inhibit conifer seedling survival except on rotted logs and other micro-mounds.

Figure 6. Number of species (richness) by age of overstory. (Curve fitted by least squares, $y = 18.4 + .527$, $R^2 = .01$. Not significant at $\alpha = .05$; $S_3 = 5.54$.)

Some small (*ca.* 10 cm high) seedlings of *Thuja plicata* and *Pseudotsuga menziesii* were randomly scattered throughout the drier part of one stand (age 11). The *T. plicata* seed source was nearby. The general absence of mature *T. plicata* and *T. heterophylla,* however, was conspicuous on floodplains and river bottoms throughout the Alsea River drainage, as was the absence of their tolerant seedlings from the understory of most red alder stands.

Would these conifers be able to replace red alder as the dominant overstory species? There is very little affirmative evidence. Since red alder is a relatively short-lived species (Fowells, 1965), the chronosequence sampled here extends to the old or mature stage of red alder and there is still very little evidence to suggest that succession will proceed toward a conifer-dominated community.

Percent crown closure of the alder canopy shows a significant ($\alpha = .05$; $S_e = 2.73$) decrease with time ($R^2 = .96$) (Fig. 8). Projecting this regression ($Y - 102 - .65x$) to zero percent crown closure indicates that the canopy should have completely deteriorated by 160 years. According to Fowells (1965), the maximum age for alder is

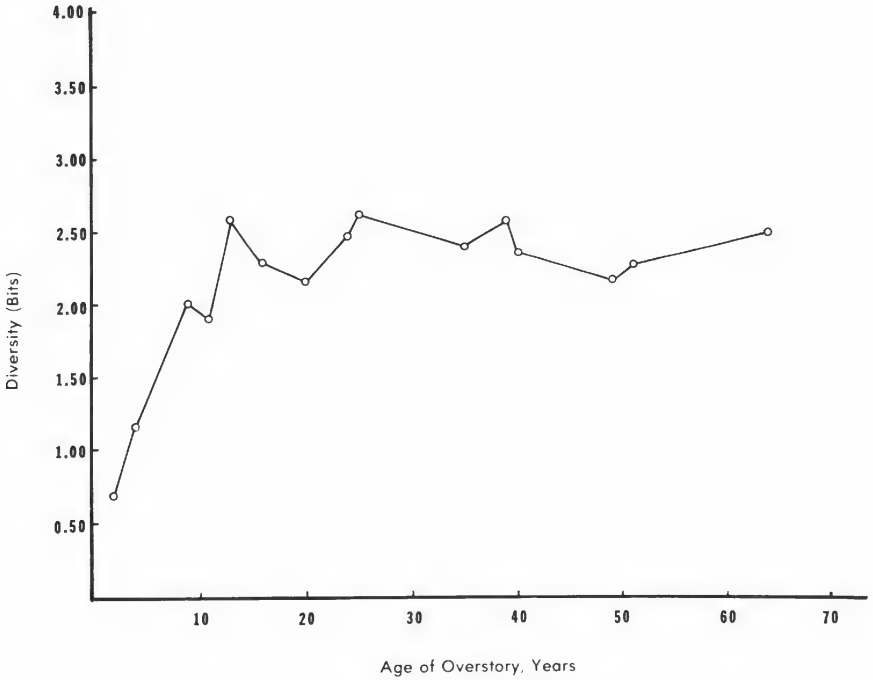

Figure 7. Species diversity (equitability) by age of overstory.

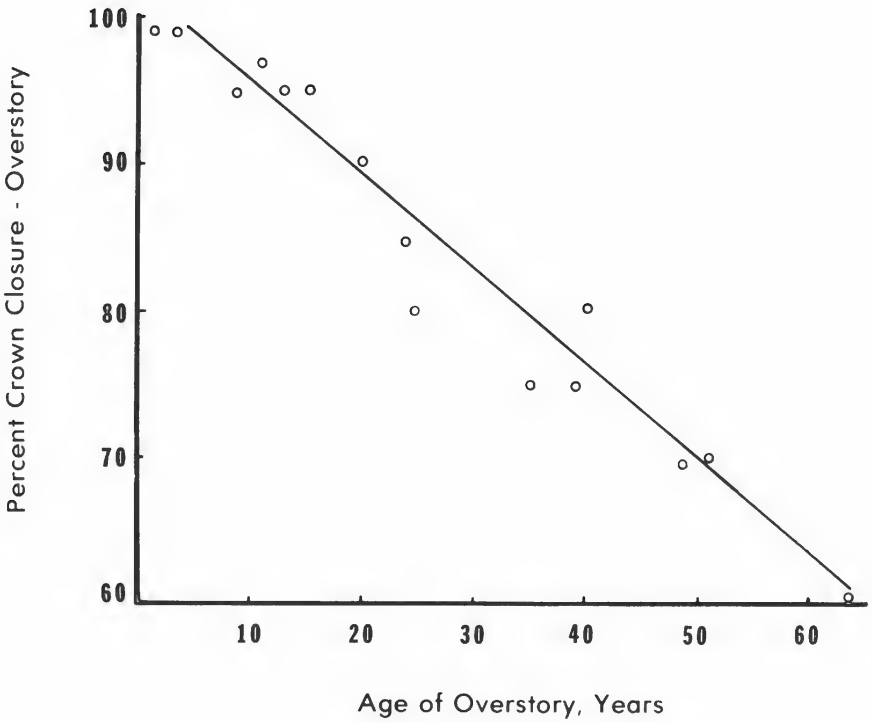

Figure 8. Crown closure of overstory by age of stand. (Curve fitted by least squares, $y = 102 - .65x$, $R^2 = .96$. Significant at $\alpha = .05$, $S_e = 2.73$.)

100 years. The maximum age of red alder on these sites therefore is about 100-160 years. What happens to the sere after 160 years in the absence of disturbance can only be speculated. It does seem likely that these sites could then be dominated by *Rubus spectabilis* and *Polystichum munitum.*

Percent of full sunlight passing through the canopy of each stand is presented in Figure 9. The linear regression calculated for these data yielded a much weaker yet still significant relationship at $\alpha = .05$ and where $S_e = 2.06$ and $R^2 = .48$.

Conclusions

The composition and structure of a chronosequence on the *Alnus rubra/Rubus spectabilis* habitat type changed considerably over the 64 years of development. Overstory structure progressed from young, dense, and even-aged stands to stands with fewer and larger stems, and a more open canopy. (See Zavitkovski and Stevens, 1972, for further dis-

Figure 9. Percent of sunlight transmitted through the overstory canopy by age of stand. (Curve fitted by least squares, $y = 4.17 + .87x$, $R^2 = .48$. Significant at $\alpha = .05$; $S_e = 2.06$.)

cussion of the overstory component.)

Understory vegetation at early stages in this succession is characterized by low species diversity and dominance by weedy grasses and forbs such as *Holcus lanatus, Stellaria media, Montia sibirica, Digitalis purpurea, Rubus ursinus,* and *Stachys mexicana.* Later stages are characterized by higher but declining diversity and dominance by shrubs and ferns such as *Rubus spectabilis, Polystichum munitum,* and *Athyrium filix-femina.*

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Literature Cited

Baldwin, E. M. 1964. Geology of Oregon. 2nd ed. University of Oregon Bookstore, Eugene. 165 pp.
Brillouin, L. 1962. Science and Information Theory. 2nd ed. Academic Press, New York. 35 pp.
Corliss, J. F., and C. T. Dyrness. 1965. A detailed soil-vegetation survey of the Alsea area in Oregon Coast Range. *In* C. T. Youngberg (ed.), Forest Soil Relationships in North America. Oregon State University Press, Corvallis.
Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northw. Sci. 33:43-64.
Fowells, H. A. (Comp.) 1965. Silvics of Forest Trees of the United States. Agriculture Handbook No. 271. U.S. Department of Agriculture, Washington, D. C. 762 pp.
Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. Portland, U.S. Pacific Northwest Forest and Range Experiment Station, Research Paper GTR-PNW-8. 417 pp.

————, and A. A. Pechanec. 1968a. Comparison of vegetation in adjacent alder, conifer, and mixed alder-conifer communities. I. Understory vegetation and stand structure. Pp. 37-44. *In* Biology of Alder, ed. by J. M. Trappe, *et al.* Portland, U.S. Pacific Northwest Forest and Range Experiment Station. 292 pp.
Friend, D. T. C. 1961. A simple method of measuring light value in the field. Ecology 42:577-580.
Hurlbert, S. H. 1971. The nonconcept of species diversity: A critique and alternative parameters. Ecology 52:577-586.
Margalef, R. 1968. Perspectives in Ecological Theory. University of Chicago Press, Chicago. 112 pp.
Meurisse, R. T., and C. T. Youngberg. 1971. Soil-Vegetation Survey and Site Classification Report for the Tillamook and Munson Falls Tree Forms. Oregon State University, Department of Soils, report to Publishers Paper Co. 116 pp.
Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-270.
Sharpe, G. W. A Taxonomical-Ecological Study of the Vegetation by Habitats in Eight Forest Types of the Olympic Rain Forest, Olympic National Park, Washington. University of Washington, Seattle, Ph.D. thesis. 335 pp.
U.S. Department of Agriculture. 1975. Soil Survey of Benton County, Oregon. 119 pp.
U.S. Department of Commerce. 1960. Climatography of the United States. No. 60-35, Climates of the States: Oregon. 20 pp.
Zavitkovski, J., and R. D. Stevens. 1972. Primary production of red alder ecosystems. Ecology 53:235-242.

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Auxin Regulation of Branch Abscission by Aspen (Populus tremuloides, Michx.)

Abstract

Populus tremuloides, Michx. abscises branches under natural conditions. Removing buds and/or leaves from a twig stimulates its abscission. The stimulation is increasingly inhibited by application of lanolin pastes containing respectively 0, 0.01, 0.1, or 1 percent indole-3-acetic acid to the cut end of a twig.

Introduction

Almost any plant part may be abscised: leaves, fruits, flowers, flower parts, bark, buds, branches, roots, or prickles (Addicott, 1965). Millington and Chaney (1973) review the rather sparse literature on branch shedding; the phenomenon is widely distributed among both angiosperm and gymnosperm families, its anatomy is similar to that associated with abscission of leaves, it occurs most often in mature trees, and it is apparently stimulated by factors producing negative carbohydrate balances in the twig; i.e., by shading, insect attack, water stress, or fruiting. Recent reviews of the physiology of abscission ignore the subject of branch shedding.

This note reports the abscission of branches in aspen (*Populus tremuloides, Michx.*) and gives evidence for control of abscission by auxin.

Methods

A set of six small twigs on one-year-old wood of an aspen branch were treated: the first four were cut back to about 1.5 cm, the fifth was defoliated and the six was half defoliated. The tips of the four clipped twigs were coated with lanolin enriched with 0, 0.01, 0.1, and 1 percent of auxin (indole-3-acetic acid), respectively. The twigs were observed at intervals to determine when they had dropped or would drop at a touch. Treatments five and six were omitted in experiments one, two, and four, described below.

Results

Experiment I. Ten sets of twigs (i.e., the first seven lateral twigs on ten branches) were treated on 20 February 1971 and observed monthly. Most fell between 30 April (69 days) and 30 May (99 days) when the trees were just leafing out (20 May). Falling later (30 June to 1 October) were one treated with pure lanolin, one treated with 0.01 percent auxin, two treated with 0.1 percent auxin, and four treated with 1 percent auxin.

Experiment II. Ten sets of twigs were treated on 6 June 1971 and observed monthly. Six of the twigs treated with unenriched lanolin dropped before 29 June (23 days) as did one twig treated with 0.01 percent auxin. The remaining twigs, excepting one,

fell by 10 August (65 days). The final twig—one treated with 1 percent auxin—fell in September.

Experiment III. Fourteen sets of twigs were treated on 29 June 1971 and observed at two day intervals through 16 August. The results are shown in Table 1.

Experiment IV. Fourteen sets of twigs were treated on 1 October 1971 and observed at monthly intervals. None had been shed by 2 April 1972 (184 days). Two (pure lanolin and 0.01 percent IAA) were shed by 16 April (200 days). On 16 April, the tips of twigs on half the branches were clipped off and fresh IAA in lanolin was supplied. Twigs with applications of less than 1 percent IAA were all abscised by 4 June (247 days). Of the branches treated with 1 percent IAA—lanolin, those receiving only the initial treatment were shed before 4 June; half of those receiving the second treatment were shed after 4 June, and 25 percent were shed after 3 July (276 days): all were shed by 3 August (307 days).

TABLE 1. Results of experiment III: retention times (days) for twigs treated on 29 June 1971 (N=14).

Treatment	median (days)	range (days)	Percent retained[1]
0.0 percent auxin	15 A	13-21	0
0.01 percent auxin	16 A	13-27	0
0.1 percent auxin	27 AB	25-37	0
1.0 percent auxin	41 AB	27-115+	29
all leaves off	37 AB	29-115+	7
½ leaves off	79+ B	37-115+	29
control	115+ B	37-115+	71

[1]Percentage of twigs retained past 23 October or 115 days.

A—Significantly different from the untreated control at the 1 percent level, Rank T-Test (Moroney, 1951).

B—Significantly different from the 0 percent auxin treatment at the 1 percent level, Rank T-Test.

Discussion

The third experiment (Table 1) shows that in summer (29 June) aspen twigs with buds removed will be abscised within 15 to 20 days and that abscission can be delayed by providing an auxin supply. That leaves may supply the auxin which naturally inhibits branch drop is suggested by the fact that defoliated and partially defoliated branches show a strong tendency to abscise.

The second experiment (6 June) shows that spring abscission rates are similar to those of mid-summer.

The first experiment (20 February) shows that the abscission rate is considerably slower in winter (70 days or more) and perhaps even nonexistent since treated twigs did not drop until spring. The fourth experiment (1 October) confirms that abscission rates are very slow in winter (200+ days). Perhaps the morphogenetic processes of abscission layer formation (cf. Eames and McDaniels, 1947) cannot occur at winter temperatures; more likely they are simply not initiated. Twigs which might have undergone abscission without treatment should have done so before 20 February or 1 October treatments; if they did not, their abscission was also prevented by winter.

The results presented above support the model that abscission occurs when auxin levels on the distal side of a prospective abscission layer are lower than those on the

proximal side (Addicott, 1961). Auxins are synthesized at and transported downward from leaves and buds. In summer, branches without leaves or buds are shed because their auxin levels are lower than trunk levels. Abscission may be inhibited by providing the branches with an auxin source: IAA rich lanolin. The absence of twig abscission in winter may be due to the weakness of auxin synthesis and auxin gradients or to low temperature inhibition of the abscission process. With the coming of spring and new auxin synthesis, budless or leafless branches are quickly shed unless they are well supplied with IAA.

Abscission of budless and leafless twigs could probably have been further postponed by continual reapplication of IAA. The poor success of such a reapplication (Experiment IV—spring, 1972) is likely due to its being made too late. The appearance of leaves soon after the reapplication suggests that buds were active at or before the reapplication time, that auxin synthesis processes were active, and that the abscission process had been initiated in most branches. Budless twigs of experiment IV which were not shed immediately (i.e., those in which abscission had probably not been initiated) were retained for over a month of "leaf time," as were summer-treated twigs of experiment III.

Literature Cited

Addicott, F. 1961. Auxin in the regulation of abscission. Encyclopedia of Plant Physiology 14: 829-838.

———. 1965. Physiology of abscission. Encyclopedia of Plant Physiology 15(2): 1094-1196.

Eames, A., and L. McDaniels. 1947. An Introduction to Plant Anatomy. McGraw Hill, New York. 427 pp.

Millington, W., and W. Chaney. 1973. Shedding of Branches. *In* T. Kozlowski (ed.) Shedding of Plant Parts. Academic Press, New York. 559 pp.

Moroney, M. 1951. Facts from Figures. Pelican, Baltimore, Md. 472 pp.

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Argumentation, Imagery, and the Original Vertebrate Habitat

Abstract

There is currently a consensus among zoologists that the first vertebrates arose in salt water. Physiological and paleontological arguments once given in support of a freshwater origin have been discounted, often with suspicious if not specious reasoning; and the earliest ostracoderms are now assigned to shallow seas. If the protochordate ancestors of these ostracoderms entered fresh waters via psammolittoral and ground water communities, rather than via estuaries, then many of the arguments in favor of a freshwater origin become convincing. Until now, however, the freshwater school has unquestioningly accepted the old poetic theory that the first fish form arose in response to stream currents.

Introduction

Some arguments, especially those with the worst prospects for solution, possess a lasting fascination. During the last seventy-five years, one such argument has developed as to the original habitat of vertebrates: did they live first in fresh or in salt water?

Until the late 1950s the champions of a freshwater origin carried the field. Either knowingly or unknowingly, many of their convictions were based on certain observations recorded in 1900 by T. Chamberlin, a far-ranging geologist who held that: "The form and motion of the typical fish are a close imitation of the form and motion of wisps of water grass passively shaped and gracefully waved by the pulsations of the current." Chamberlin then proceeded to charge his hypothesis with more scientific, or at least less poetic, speculation:

> "It is not difficult for the imagination to picture a lowly aggregate of animal cells, still plastic and indeterminate in organization, brought under the influence of a persistent current and caused to develop . . . a spindle-like form, a lateral flexibility, and a set of longitudinal side muscles adapted to rhythmic contractions. . . . The rhythmical undulations of the lamprey which perhaps best illustrates the primitive vertebrate form, and is itself archaic in structure, are an almost perfect embodiment in the active voice of the passive undulations of ropes of river confervae. . . . The two phenomena are natural reciprocals in the active and passive voice."

Duke Ellington once said of Ella Fitzgerald that she affects you through the facets of your intangibles. Dr. Chamberlin, no master of scat, nevertheless voiced an argument whose force was as much connotative and imagistic as it was denotative. Even though imagery has become a rare fish in twentieth century scientific prose, we can find Chamberlin's observations serving as the source, or the prototype, for more recent statements. Witness A. S. Romer, who says in the 1966 edition of his *Vertebrate Paleontology:* "The active swimming characteristics of vertebrates suggest that their home lay in fresh waters where mobility was necessary to counteract the downward sweep

of stream currents." Or you can turn to a more popular writer, Rachel Carson, and find that: "Fish, tapered of body and stream-molded by the press of running waters, were evolving in Silurian rivers."

Professor Romer was among the first to support a freshwater origin with fact as well as hypothesis. In the 1930s he and his students examined the oldest known vertebrate remains, which came from the Middle Ordovician Harding Formation in Colorado. These fossils, consisting of fragments of dermal bone, by themselves were not very informative, but the accompanying invertebrate fossils of worm borings, snails, clams, and lamp shells told of a deltaic or near-shore marine environment. Romer took this evidence, juxtaposed it with some intriguing negative data, and deduced a freshwater origin to scientific satisfaction. This piece of reasoning, although a little oily, remains potent. He said, in essence: 1) only marine and estuarine fossils are known for the Ordovician, whose continental deposits have since been reworked and destroyed by episodes of mountain building and erosion; 2) in the Silurian, when freshwater deposits do appear in the fossil record, vertebrates are in them; 3) therefore, although the first vertebrates lived in freshwater, evidence of them is now restricted to their accidental inclusion in marine deposits; 4) the estuarine, deltaic, and sublittoral sites that now yield bones of the first vertebrates received them because of post-mortem transport —the fish died, bloated, floated, and were ultimately deposited downstream where the rivers met the seas.

Fossils of the earliest known vertebrates consist of disarticulated and fragmented bones only, thus reconstructions of their form are little more than conjectural. Probably they did not much resemble fish. According to most interpretations, they lacked jaws, they lacked fins, and they were encased by bones that developed in the skin, which is the rationale for their appellative, the ostracoderms (shell + skin). Articulated fossils are known from the late Ordovician and early Silurian, and these show animals with paired dorsal as well as lateral eyes, tails whose axis curves either upward or downward, and a body compressed from top to bottom or from side to side. The articulated fossils are of fish rarely longer than a foot. Some lived on the bottom, whereas others inhabited midwaters.

Romer knew how to fortify an argument with battlements visible for miles and years around. After stressing the absence of Ordovician continental deposits, and after surmising that the mobile ostracoderm form was an adaptation to stream currents, he began to speculate on the armor of the first vertebrates. He asked what force of natural selection would have favored that bony panoply, and he summoned up an answer: eurypterids. Of all the arthropods to appear over the ages, eurypterids were the biggest. Ten feet long and resembling scorpions, they plied the predatory niche of the early Paleozoic Era. Romer and others, construing these arthropods as the ancestors of terrestrial scorpions, supposed they had entered fresh waters where they preyed upon ostracoderms. In fact, Silurian deposits known to represent freshwater sites do include assemblages of eurypterids and ostracoderms. Romer concluded in 1933 (and many times afterward) that vertebrate armor arose in response to eurypterid predations.

Physiologists added support to the freshwater school in the early days of the argument. Homer Smith, an essayist, philosopher, and novelist as well as a renal physiologist, interpreted the appearance of bony armor in a new light. He saw it as an adaptation to reduce loss of water across the skin. In a marine world, where salts of the sea and

of the organism register about the same, no salt or water-regulation problems plague animals; but in fresh water, the tendency to gain fluids and lose solutes proves lethal in the absence of compensatory adaptations. So, according to Smith, the armor helped seal off the first vertebrates from osmotic stresses of their freshwater environment. He conceded that the armor might also have protected them against eurypterids, and perhaps it served as a mineral reservoir when phosphates and the like were in short supply.

The really ingenious physiological argument for a freshwater origin, also developed by Homer Smith, centered on the vertebrate kidney. In a series of articles stretching from the 1930s into the 1960s, Smith examined the structure and function of kidneys in diverse sharks and skates, lungfish, bony fishes, and a grand sampling of tetrapods. Some of his research was of the applied sort, and no doubt he has furthered our understanding of humans in health and in disease; but Smith believed unabashedly that the evolutionary story merited equal study, and that animal adaptations are interesting in their own right, without being dignified by that grant-getting, ungrammatical addendum: "From such investigations we hope to gain a more complete understanding of man." One of the things that continued to engage him was the similarity of nephrons among vertebrates. These fundamental units of the kidney generally consist of a capillary tuft (the glomerulus) in which blood pressures drive fluids and small molecules from the vessels, an encircling capsule that collects the filtrate, and a tubule whose walls reabsorb some substances (water, salts, sugars) and excrete others (various metabolic end-products), thereby converting the filtrate to urine. Of course Smith observed variations on this pattern. For example, in hagfish and certain other primitive forms, the capillary tufts sometimes fuse to form a glomus, whose filtrate is deposited in the body cavity; there, it is swept up by a rudimentary tubule known as a ciliated nephrostome. In land-going vertebrates, urine processing becomes very complicated: the tubule is differentiated into proximal and distal portions, and it may acquire long loops of Henle that further concentrate the fluid. But in the nephrons of all classes, a filtrate-forming capillary tuft develops and is the essence of the vertebrate pressure-type kidney.

This glomerulus puzzled Smith. Although he realized that evolution rarely proceeds prudently along orthogonal lines, he wondered what selection pressures would have favored a kidney such as his own that poured out the body's vital contents sixteen times per day, then caught them before they hit the ground. He resolved the problem with a compelling explanation. The first vertebrates must have evolved in fresh water where their bony armor served imperfectly as a shield against osmotic stress—after all, a flow of water across the gills had to be maintained, and water must occasionally have been swallowed with food. Consequently, a continuous influx of fluid and leeching of salts threatened to liquefy them. The glomerulus was thus a means of pumping out the water shipped by ostracoderms. Meanwhile, tubular reabsorption salvaged needed salts.

One's predictable objection here is: if glomeruli are freshwater adaptations, then how do modern fish manage to inhabit the seas? Like Romer, Smith was a believer in negative and oblique data. Accordingly, he pointed out that the existence of glomeruli in all vertebrate groups, including primitive jawless and jawed forms, indicated these kidney components were present at the inception of vertebrates. Moreover, the osmoregulatory modifications seen in marine fishes are evidence of a long struggle with their glomerular heritage. Examples of these modifications are several and diverse. In the hagfish, salt is retained so that animal and ocean are equally salty. In sharks, skates,

and chimaeras—the cartilaginous fishes—urea is retained in concentrations two-hundred fold greater than in other fishes; as a result, they are slightly hypertonic to salt water, causing an inward osmotic gradient that furnishes their glomeruli with water to pump. Sharks and rays are additionally adapted to the seas by virtue of their rectal gland, a little sausage-shaped structure used to remove excess sodium chloride from the blood and discard it via the intestine. Bony marine fishes have grappled with their glomeruli by reducing them, by eliminating them, by depressing the rate of urine formation because of increased reabsorption, and by excreting excess salt at the gills. Plainly, glomeruli have had to be reckoned with in a marine environment.

The contentions of Romer, Smith, and their respective schools appeared as textbook truths through the 1930s, '40s, and '50s. During this time, objections from saltwater factionists rose no higher than footnotes and minor articles. Then, in 1956, the paleontologist R. H. Denison published a major review on the habitat of early vertebrates. Whereas Romer relied on inspired argumentation, Denison used strings of facts to build his case. The conflict pitted creator against critic, right hemisphere against left hemisphere.

Denison re-examined ostracoderm fossils from the Harding Sandstones of Colorado and adjacent areas. Still older Ordovician fossils from the Glauconite Sands of Russia had been discovered since Romer's 1930's articles, and Denison also inspected these shards of dermal bone. He then based his rebuttal on five points. First, the unnatural abundance of fragments disagreed with post-mortem transportation of floating corpses. Second, these fragments are around one inch in diameter, but the well-sorted sand grains of the fossil sites indicate the current was incapable of carrying such fragments in suspension. Third, the fragments show slight wear, hence were not transported very far on stream bottoms. Fourth, distribution of these fragments is not local—they occur abundantly over large areas, including Colorado, Wyoming, and South Dakota in the United States, and over a comparable area in Russia. And fifth, the Glauconite Sands of Russia very possibly represent a typical marine formation rather than a deltaic deposit.

Although Denison's case was inconclusive, his review was long, his tone certain, and his stature considerable. Biologists listened. Perhaps, too, the time was ripe, for a number of articles followed hard upon his ground-breaker, including major works by J. D. Robertson in 1957 and E. I. White in 1958.

Robertson agreed with Denison that the first vertebrates occupied marine waters, where he pictured them grubbing in the offshore mud. He extended the argument by examining ostracoderm deposits of the Silurian Period. Many of these more recent forms undoubtedly occurred in fresh water and were part of an adaptive radiation there. Noting that all modern fish, with the exception of hagfish and the urea-retaining cartilaginous species, are one-third to one-fourth as salty as the seas, Robertson made two proposals: 1) the original vertebrates, whose stock persists today as hagfish, lived in the seas and were isotonic with their environment, as are practically all marine invertebrates; 2) all other extant fish evolved from Silurian stock that had entered fresh waters where their salt levels fell irreversibly.

E. I. White subscribed mostly to the Denison-Robertson school of saltwater origin, but he departed importantly from the usual arenas of the argument by asking for a definition: at what point did the protochordate ancestor of those first vertebrates be-

come a vertebrate? That those ancestral protochordates resided in salt water is not disputed. They were soft-bodied, small filter-feeders, no doubt isotonic to salt water, as are their living kin the sea squirts, lancets, and acorn worms. They were also invertebrates in the sense that they lacked vertebrae. However, no vertebrae have been described for ostracoderms either, so we cannot in good conscience use the acquisition of these bony axial supports to define the first vertebrate. Probably the formation of a carapace of dermal bone serves best to distinguish vertebrates from protochordates, along with greater cephalization and reliance on muscular as well as ciliary ingestion. These features, being difficult to measure and to document in the fossil record, make drawing the line between groups a subjective act. What we can be sure of, said White, is that marine protochordates gave rise to vertebrates, whose home was soon, although not originally, in fresh water.

Romer's claim that ostracoderm armor arose in fresh water as a defense against eurypterid predations suffered attrition from several criticisms in the 1950s and 1960s. It became apparent that eurypterids did not achieve numerical success and prodigious size until the Silurian Period. Earlier, in the Ordovician, they were small, scarce, and inconsequential predators. Still earlier, in the Cambrian, when bony dermal armor probably first appeared, eurypterids had not broken off from their trilobite ancestors. Undaunted, Romer restated his hypothesis in 1968, and again in 1970, studiously ignoring the mounting objections.

Homer Smith's glomerular logic fell into disfavor as Romer's paleontological proofs wore thin. The arguments against Smith came from all directions and were not always seaworthy. Denison suggested that the first vertebrates were saltier than sea water, as are modern urea-retaining fishes, thus the glomeruli would still have functioned in eliminating excess water. As early as 1954, Robertson denied that the primary function of the glomerulus was filtration on the grounds that many primitive fishes have low blood pressures incapable of driving fluids out of the capillaries, a statement since proved specious. In 1967, G. S. Carter took a broader if equivocal view by interpreting the kidneys of marine fish as part of a successful system for ionic and osmotic regulation; in his scheme, excretion of ions by the gills, selective reabsorption and excretion by the kidney tubules, altered permeability of the integument, and drinking behavior interact to maintain a constant internal environment, and individually are without evolutionary implication. Leonard Kirschner, in 1967 and as the invited speaker at a Washington State University address in 1972, praised the ingeniousness of Smith's arguments but called attention to several marine invertebrates, such as clams and polychaete worms, whose pressure-type kidneys form and reabsorb filtrates. Arguing by analogy, Kirschner saw no reason to suppose glomeruli could not have evolved in the oceans, albeit vertebrates are neither worms nor clams, and quite obviously marine fishes have had to live with their glomeruli by means of sundry innovations. The most recent rejection of Smith's interpretations was made in 1975 by K. Schmidt-Nielsen, who flatly stated that physiological characteristics have no place in evolutionary inferences. His reasoning: physiological characteristics evolve more rapidly, and are more prone to convergent evolution, than are morphological characteristics. This evolutionary opportunism makes them unreliable as indicators of what was. So, to say that glomeruli have always functioned in filtrating excess water is unjustifiable. Rarely does Schmidt-Nielsen deliver such dogma.

Neither Romer nor Smith engaged the saltwater contingent in point-by-point criticisms. Before dying both men expressed a continuing belief in their freshwater arguments but admitted that the work of Denison and his followers merited serious study. No doubt a banner with the colors of Romer and Smith is borne somewhere on the horizon. At the moment, however, salt water is in the ascendance. Even textbooks are now finding Ordovician ostracoderms in shallow seas and along coastlines of ancient continents.

The history of ideas is an untidy one. They may develop in logical sequence, or in opposition to each other, or as renegades from the inscrutable unconscious. They will, in any case, stubbornly refuse to leap certain barriers, especially in sustained formal arguments where the trackways deepen over the years. For example, in the present argument only one route is permitted for entry into fresh waters: the ancestors of vertebrates swam from the seas into bays and thence up rivers (and in so doing acquired a spindle-like form, a lateral flexibility, etc.). No one has asked whether they might have followed a different passageway—a preposterous suggestion, to be sure.

Entry of marine invertebrates into fresh water apparently has not occurred by a single route only. Freshwater mites, pulmonate snails, and aquatic insects, for example, hail from ancestors who somehow left the seas for the shores, then travelled overland and eventually reinvaded water, this time fresh. Some crustaceans have crawled over the ages up estuaries, gradually adapting to brackish and then to fresh habitats—the Chinese mitten-handed crab appears to be penetrating fresh water in just such a fashion even now. The most heavily travelled route, however, has been an obscure, recently noticed one. It involves the fauna of sandy beaches. There, little invertebrates, some of them microscopic, form a teeming community dwelling in the watery interstices between sand grains. Protozoans, rotifers, water bears, coelenterates, flatworms, ribbonworms, round worms, annelids, molluscs, arthropods, pogonophorans, chordates—all major and most of the minor phyla have representatives here, in what is referred to as the psammolittoral community. These minute animals find themselves within a few feet of fresh water along the landward margins of beaches, where ground water meets sea water. In this narrow zone excursions from high to low salinities are common among many animal populations, and the crossing and adaptation to fresh ground water appears to have happened frequently in terms of geological time. Advantages of this passageway over estuarine or overland routes are several. In particular, the brackish zone is brief, the salinity gradient gradual, the temperature constant, and the opportunity to retreat safely after an exploratory foray maximal. In addition, the animals are not exposed to the currents of estuaries, the wave action of the intertidal zone, or the sun and air of the uplands.

There is now fair agreement that most of the invertebrates in our modern freshwater fauna had psammolittoral ancestors who entered ground water and, once there, experienced a complex of adaptations. In particular, the salt concentrations of their plasma dropped to one-third that of marine kin, and they acquired protective cuticles for excluding water and some sort of nephric device for expelling fluids. From ground water the invertebrates passed inland via freshwater sandy beaches to lakes, and from lakes to streams, where another set of adaptations evolved that allowed them to live in currents.

If the psammolittoral passageway served so well for invertebrates, might the lineage culminating in vertebrates have used it also? What was there about vertebrates that

could have closed this way to them? And why has a psammolittoral origin not been presented as a possibility for them? To answer these questions, a review of vertebrate precursors is necessary.

In the nineteenth and early twentieth centuries several invertebrate groups were postulated as ancestral to the Phylum Chordata, which comprises vertebrates plus their spineless cousins (sea squirts, lancets, and possibly acorn worms). They included spiders, horseshoe crabs, scorpions, and worms, to name the most ardently proposed groups. None of these proved to have a convincing claim when examined closely. Hearts occurred in the wrong places, blood flowed the wrong way, notochords and gill slits were lacking, and nerve cords were not hollow or else they ran along the stomach rather than the back.

The Phylum Echinodermata, including starfish, sand dollars, sea urchins, sea lilies and sea cucumbers, eventually surfaced as the best candidate for the phylogenetic parent of chordates. Members of this improbable consort resemble chordates not in their adult but in their *larval* stages. Unlike the brainless, pentamerous, sedentary adults, the larvae are mobile, bilateral, and equipped with sense organs for sampling prospective settlement sites. Moreover, the body cavities of primitive chordate and echinoderm larvae develop as pouch-like outgrowths of the alimentary tract, and their blastopore—the original hole leading into the alimentary canal—becomes the adult anus, whereas in most other groups it becomes the mouth.

Furthermore, echinoderms and chordates have been related by the presence of an intermediary. The relationship depends on acorn worms. These worms are placed either with the chordates by virtue of their adult gill slits, dorsal nerve cord, and suggestion of a notochord, or they are assigned to an allied phylum, the Hemichordata. The larvae of acorn worms, however, are remarkably like certain echinoderm larvae: both show the same pattern of ciliary tufts and tracts, both show alimentary pouches that agree in number and locations, and both have the same general form.

Now we approach a motif of chordate evolution: major phyletic departures build on larval forms, not on adults. A paradigm for this motif involves the spineless chordates known as sea squirts. In the adult stage these primitive chordates are filter-feeders, without mobility, without notochord, without nerve cord. The larvae, in contrast, are tadpole-like and have nerve cord, notochord, and a muscular tail for locomotion. The larvae may be additionally equipped for the active life because of rudimentary eyes and otocysts. Sea squirt larvae function in dispersing the species, and their lifespans usually are brief.

Here is the paradigm. Several evolutionists (including Romer, 1955) have pointed out that the larvae of ancient, filter-feeding chordates were not realizing their evolutionary potential because they failed to occupy the adaptive zone open to animals able to locomote. No doubt such forms function well in scattering adults of a species, but might they become greater successes as their own species? If, in an evolutionary sense, the child could father the man, what might result from these tadpoles? Paedogenesis, or maturation in the larval stage, is the developmental trick responsible for this transformation. In this event the gonads mature during larvalhood, causing somatic differentiation to cease and thereby preventing metamorphosis into a sedentary, continuously feeding adult. Such a mechanism not only furnishes reproducing species with

a new form, it also lops off the terminal, most specialized stages of an animal's life and renews evolutionary plasticity in the phylum.

Again, why wouldn't the psammolittoral passageway have proved suitable for those Cambrian larvae that were to found the vertebrate lineage? Isn't it plausible that those paedogenetic tadpoles slithered between sand grains, advancing into brackish and then into fresh waters, where they acquired dermal armor and a glomerular, water-excreting kidney? Isn't it more plausible than an upriver route? After all, the first vertebrates were small animals encumbered by a jacket of bone—how could they have swum like salmon against the current? So, why has the psammolittoral route been ignored?

"The form and motion of the typical fish are a close imitation of the form and motion of wisps of water grass passively shaped and gracefully waved by the pulsations of the current."

"*Wisps of water grass. . . .*"

"Fish *stream-molded* by the press of running waters, by the *downward sweep* of waters. . . ."

"*Stream-lined* fish . . ."

Very likely many of our theories, which seem based on careful evaluation of fact, are tenaciously defended because of the insidious persuasion of unconscious images. We are affected through the facets of our intangibles.

If the psammolittoral route is given proper consideration, then many of the arguments of Smith and Romer may be re-evaluated and found credible. The freshwater school, a sleeping giant, begins to stir.

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Literature Cited

Carson, Rachel. 1950. The Sea around Us. Oxford Univ. Press, New York. 230 pp.
Carter, G. S. 1967. Structure and Habit in Vertebrate Evolution. Univ. of Washington Press, Seattle. 520 pp.
Chamberlin, T. C. 1900. On the habitat of the early vertebrates. J. Geology 8: 400-412.
Denison, R. H. 1956. A review of the habitat of the earliest vertebrates. Fieldiana: Geology 11: 359-457.
Kirschner, L. B. 1967. Comparative physiology: invertebrate excretory organs. Annual Rev. Physiol. 29: 169-195.
Robertson, J. D. 1954. The chemical composition of the blood of some aquatic chordates. J. Exp. Biol. 31: 424-442.
———. 1957. The habitat of the early vertebrates. Biol. Reviews 32: 156-187.
Romer, A. S. 1933. Eurypterid influence on vertebrate history. Science 78: 114-117.
———. 1955. The primitive vertebrate as a dual animal—somatic and visceral. Proc. Zool. Soc. London 125: 811.
———. 1966. Vertebrate Paleontology. Univ. Chicago Press. 468 pp.
———. 1968. Notes and Comments on Vertebrate Paleontology. Univ. Chicago Press. 304 pp.
———. 1970. The Vertebrate Body. W. B. Saunders Co., Philadelphia. 601 pp.
Schmidt-Nielsen, K. 1975. Animal Physiology. Cambridge Univ. Press, London and New York. 699 pp.
Smith, H. W. 1932. Water regulation and its evolution in fishes. Quart. Rev. Biol. 7: 1-26.
———. 1932. Kamongo. The Viking Press, New York. 151 pp.
———. 1953. From Fish to Philosopher. Little, Brown and Co., Boston. 293 pp.
White, E. I. 1958. Original environment of the craniates. *In* Studies on Fossil Vertebrates (ed. T. S. Westoll). Pp. 212-234. Athlone Press, London. 380 pp.

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Frost Tolerance in Seedlings of *Vaccinium membranaceum*, *Vaccinium globulare*, and *Vaccinium deliciosum*

Abstract

Frost tolerances of *Vaccinium globulare, V. deliciosum, and V. membranaceum* seedlings were compared at controlled temperatures of 0°, −3°, −6°, and −9°C. Subsequent shoot growth decreased with decreasing temperature in all species, but growth trends differed. Seedings of *V. deliciosum* were more frost tolerant than the others. *V. deliciosum* seedlings also began spring growth earlier when all three species were grown in the same environment.

Introduction

Wild huckleberry fields occupy extensive areas in the mountains of Oregon and Washington. Many of these areas produce large quantities of high quality fruit, and some are heavily utilized by berry pickers (Minore, 1972). Unfortunately, huckleberry production is often reduced by frost damage. Similar crop reductions occur in the blueberry fields of eastern North America (Johnson, 1951; Hall, Aalders, and Barker, 1964). Sometimes most of the autumn berry crop is destroyed by spring frosts that occur when the huckleberry bushes are actively growing, but a few huckleberry shrubs remain uninjured and productive after severe frosts. Many of these shrubs escape damage because they grow in protected locations or under local heavy snow accumulations where active growth is delayed. Others seem to be frost resistant—field observations after the severe frosts of 1973 indicated that some northwestern *Vaccinium* species are more frost tolerant than others. As it is difficult to separate species differences from environmental differences in the field, we compared the frost tolerances of three common northwestern *Vaccinium* species under controlled conditions. Our working hypothesis was that frost damage would increase with decreasing temperatures. Further, we expected damage to differ among species.

Vaccinium membranaceum grows at moderate to high elevations (1000-1800 m) on both eastern and western slopes of the Olympic Mountains and the Cascade Range. *V. globulare* also grows at moderate elevations, but usually occurs east of the Cascade crest. Both *V. membranaceum* and *V. globulare* are large shrubs, 0.5-1.0 m tall when mature. In contrast, *V. deliciosum* is a low, matted shrub less than 0.5 m tall. It is common at elevations above 1300 m in the Olympics and Cascades. All three species produce palatable berries, and all three occur in the heavily used huckleberry fields near Mt. Adams, Washington.

Methods

V. membranaceum, V. globulare, and *V. deliciosum* berries were collected from the

Sawtooth huckleberry field near Mt. Adams, Washington, in September, 1974. A single shrub (the only one found in this locality) provided the *V. globulare* berries. *V. membranaceum* and *V. deliciosum* berries were collected from many (>50) shrubs. Viable seeds were obtained from these fresh berries by pulping them in a laboratory blender, then decanting the lighter pulp from the heavier seeds by running water through a gently agitated dish. After drying, the unstratified seeds were sown on moist peat surfaces in a growth chamber set for 18°C, 12-hour days and 13°C, 12-hour nights. The seeds of all three species germinated in 16 to 21 days. Seven weeks after germination, growth chamber conditions were changed to 20°C, 14-hour days and 14°C, 10-hour nights. After seedlings were 10 weeks old, the peat substrate was saturated periodically with a nutrient solution based upon the macronutrient proportions published by Ingestad (1973) and the micronutrients listed by Minton, Hagler, and Brightwell (1951).

Twelve-week-old seedlings of all three species were transplanted to individual pots filled with a peat-sand soil (50 percent peat, 50 percent soil by volume). These pots were arranged in three randomized blocks within the growth chamber. Each block contained 72 pots (24 of each species) randomly arranged by species and future freezing treatment. Temperatures, photoperiods, and nutrient additions were maintained at the levels used before transplanting. All seedlings were grown under these conditions for an additional 20 weeks. All three species responded well and appeared to be equally healthy and vigorous when 32 weeks old.

Dormancy was induced in the 32-week-old seedlings by gradually lowering growth chamber temperatures and shortening photoperiods over four weeks. (Temperatures were lowered 2.8°C, and photoperiods shortened 1.5 hours per week.) At the end of this adjustment period, temperature was maintained at a constant 3°C, with 8 hours of illumination in every 24-hour period. These chilling conditions were maintained for 16 weeks, with one exception—4 weeks into the dormancy period, a growth chamber malfunction lowered the temperature to –1°C for an unknown period during a weekend. Although both soils and plants appeared to be frozen solidly in this accidental occurrence, seedlings were not adversely affected. When growth chamber temperatures and photoperiods were readjusted to pre-chilling levls (20°C, 14-hour days; 14°C, 10-hour nights) 12 weeks later, the dormant seedlings responded by breaking buds and commencing growth.

After chilling conditions had been terminated for 10 days, the new leaves on each seedling were counted. Five weeks after chill termination, the vigorously growing seedlings were transferred to a 1°C conditioning room for 24 hours, then subjected to 1-hour freezing treatments at 0°, –3°, –6°, and –9°C. Pots were embedded in sawdust to prevent soil freezing during these treatments. Beginning at 1°C, the freezing-treatment temperatures were attained gradually by lowering air temperatures at a uniform rate of 4°C per hour in a freezing chamber. After being held at the treatment temperature for 1 hour, temperatures were raised again to 1° at the same rate of 4°C per hour (1° every 15 minutes). Six seedlings of each species were treated at each temperature —in each of the three randomized blocks. The blocks were treated sequentially in the same freezing chamber. Treatments in each block were randomly ordered and applied in successive freezing-chamber cycles. In this way, 216 *Vaccinium* plants were frozen—3 blocks x 3 species x 4 treatments x 6 seedlings per treatment.

Immediately before being subjected to the freezing treatments, the length of the longest live shoot on each of the 216 *Vaccinium* seedlings was measured and recorded. Immediately after treatment, all seedlings were transferred back to normal growing conditions in their original, randomized growth chamber positions. They were maintained in this growth-chamber environment for an additional eight weeks following treatment, after which the length of the longest live shoot on each seedling was again measured. Shoots of all seedings then were cut at the soil surface, oven-dried at 65°C for 48 hours, and weighed. Shoot response was calculated by subtracting shoot lengths eight weeks after treatment from shoot lengths immediately before treatment.

To test our hypothesis, main effects of temperature treatments and their interactions with species were partitioned into linear, quadratic, and cubic components and subjected to analyses of variance (Snedecor and Cochran, 1961, pp. 349-359). Response curve equations were then constructed for each species using as coefficients only those values that were significant at $P<.05$. Finally, the calculated curves were used to illustrate graphically any statistically significant frost response trends.

Results

Phenological differences between species became evident soon after the dormant *Vaccinium* seedlings resumed growth at the end of the chilling period (Fig. 1). *V. deliciosum* buds expanded more rapidly than buds of the other two species. Average numbers of new leaves per plant 10 days after chill termination were:

V. membranaceum—10.0
V. globulare—10.3
V. deliciosum—36.2

These differences between *V. deliciosum* and the other species are statistically significant at the .05 level of probability.

Figure 1. *Vaccinium globulare* (left), *V. deliciosum* (center), and *V. membranaceum* seedlings 10 days after termination of chilling conditions. *V. deliciosum* breaks dormancy faster than the other two species.

Seedlings subjected to 0° and –3°C treatments were not visibly affected, and shoot response did not differ appreciably among species. In contrast, frost damage was evident immediately when seedlings were removed from the –6° and –9°C treatments. Leaves were dull in color or wilted, with an odor reminiscent of fresh peas. Although all plants were injured at these lower temperatures, *V. deliciosum* seedlings seemed less affected than seedlings of the other two species. This difference between *V. delicio-*

Figure 2. *Vaccinium globulare* (left), *V. deliciosum* (center), and *V. membranaceum* seedlings four weeks after freezing at –6°C. *V. deliciosum* is less damaged than the other two species.

TABLE 1. Average **Vaccinium** shoot response (length difference) measured 8 weeks after freezing.[1]

Species	Freezing Temperature (C°)			
	0°	-3°	-6°	-9°
		cm		
V. globulare	+2.08	+2.28	-6.58	-11.75
V. membranaceum	+2.25	+1.28	-6.50	-9.22
V. deliciosum	+2.61	+3.08	-1.19	-6.36

[1]Response=length of longest live shoot 8 weeks after freezing minus length of longest live shoot before freezing. Negative values indicate shoot length decreases. Each tabular figure is the average of 18 plant measurements.

TABLE 2. Average oven-dry **Vaccinium** shoot weights measured 8 weeks after freezing.[1]

Species	Freezing Temperature (C°)			
	0°	-3°	-6°	-9°
		g		
V. globular	3.37	3.75	1.41	1.51
V. membranaceum	3.29	3.61	1.61	1.43
V. deliciosum	3.18	3.34	2.24	1.54

[1]Each tabular figure is the average shoot weight of 18 plants.

sum and the other species was quite apparent 4 weeks after treatment (Fig. 2). None of the seedlings died, and the 8-week measurements summarized in Tables 1 and 2 confirmed our earlier observations. Shoot response trends and species-treatment interactions were significant at the .001 level of probability. Temperatures of 0° and –3°C did not seem to damage any of the species. All shoot lengths were reduced by the –6° and –9°C treatments, but the species trends differed (Fig. 3). *V. deliciosum* shoot lengths were less affected by –6°C than shoots of other species. The superior frost tolerance of *V. deliciosum* at –6°C also is demonstrated by the shoot-weight trends shown in Figure 4. Both shoot length and dry weight response curves indicate converging species trends at –9°C.

Discussion

Phenological differences among species may be partially responsible for the observed differences in frost tolerance. Because *V. deliciosum* began spring growth earlier than the other species, its new leaves and shoots had a somewhat longer time to mature and harden before being subjected to the freezing treatments. All three species experienced

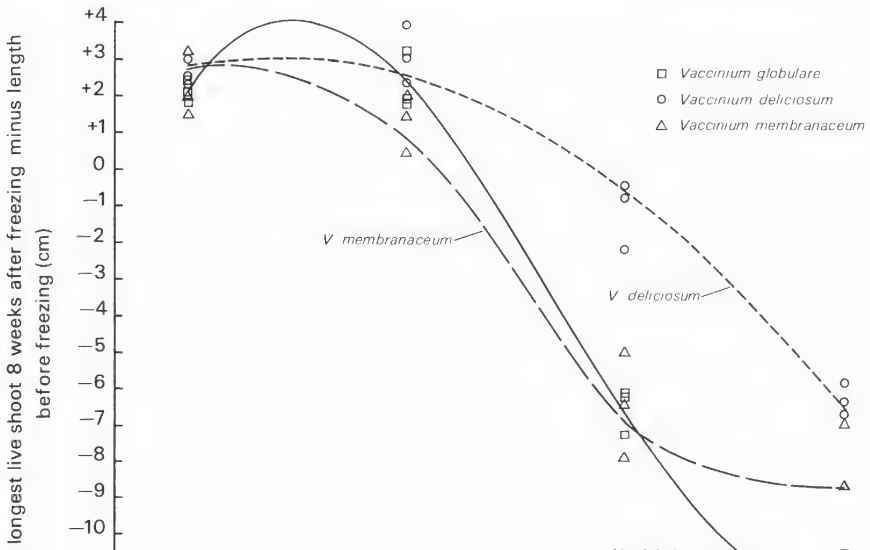

Figure 3. Response curves showing decreased growth (length difference) measured eight weeks after freezing. Each plotted point is a block average (six seedlings). Linear components of all three species trends are highly significant. Quadratic components of the *V. deliciosum* and *V. globulare* and cubic components of the *V. globulare* and *V. membranaceum* trends are also highly significant.

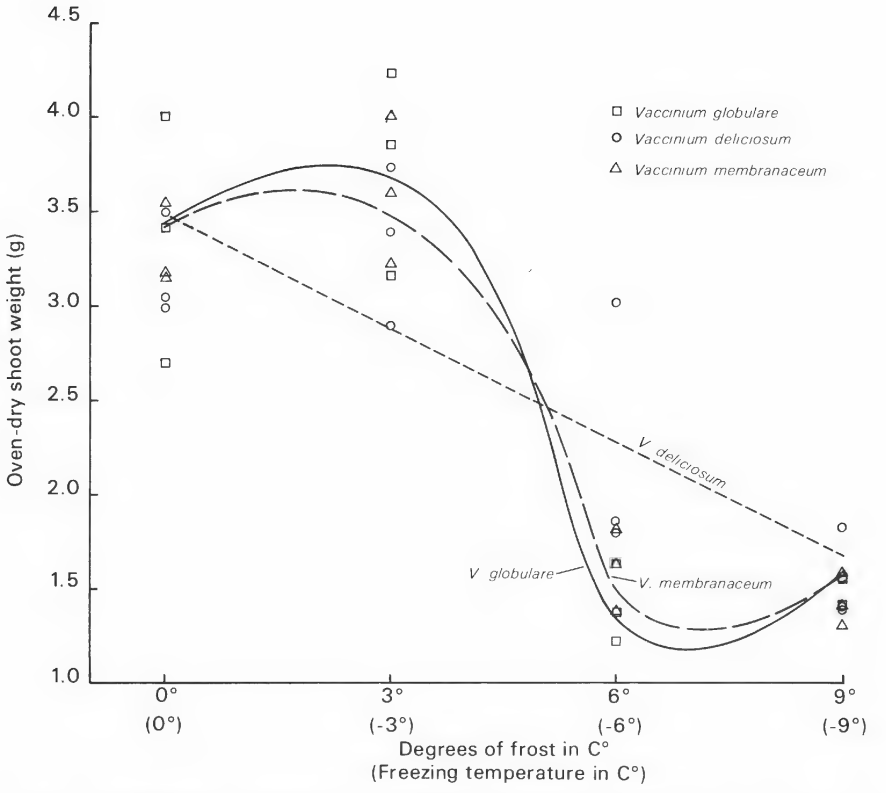

Figure 4. *Vaccinium* shoot-weight trends measured eight weeks after freezing. Each plotted point is a block average (six seedlings). Linear components of all three species are highly significant. Cubic components are highly significant in the *V. membranaceum* and *V. globulare* trends.

identical dormancy and growth environments, however, so this difference in phenology does not negate the observed frost tolerance differences as such. In nature, *V. deliciosum* should be more tolerant of spring frosts than either *V. membranaceum* or *V. globulare* when all three species have emerged from their winter dormant period. If an early spring frost struck after *V. deliciosum* broke dormancy, but before *V. membranaceum* and *V. globulare* began spring growth, the observed frost tolerance relationship among species might be reversed. This latter situation probably seldom occurs in nature, for the lower stature of *V. deliciosum* keeps it under the snow longer than the taller shrubs of *V. membranaceum* and *V. globulare,* effectively delaying its growing season. Similar stages of shoot maturity might occur in all three species simultaneously if this growing season delay in *V. deliciosum* compensated for the phenological differences among species. Our data do not permit frost tolerance comparisons in such a situation.

Growth chamber conditions and the plants growing in these conditions, though uniform and comparable, are not exactly the same as field conditions and plant ecotypes existing in nature. The absolute levels of frost response measured in our growth chamber may or may not occur at similar temperatures in nature, even when similar precondition-

ing regimes and identical rates of cooling and warming occur. The relative species differences observed here, however, should be similar to those in nature. When all three species are growing vigorously in the spring, *V. deliciosum* is more frost tolerant than either *V. membranaceum* or *V. globulare*. *V. deliciosum* probably should be favored where frost-prone areas are managed for wild huckleberry production.

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Literature Cited

Hall, I.V., L. E. Aalders, and W. G. Barker. 1964. A preliminary investigation of factors limiting lowbush blueberry production on Cape Breton Island. Can. J. Plant Sci. 44(5): 491-492.

Ingestad, T. 1973. Mineral nutrient requirements of *Vaccinium vitis idaea* and *V. myrtillus*. Physiologia Plantarum 29(2): 239-246.

Johnson, S. 1951. Problems associated with cultivated blueberry production in northern Michigan. Michigan State College Agric. Exp. Stn. Quart. Bull. 33(4): 293-298.

Minore, D. 1972. The Wild Huckleberries of Oregon and Washington—A Dwindling Resource. USDA For. Serv., Pac. Northwest For. & Range Exp. Stn. Res. Pap. PNW-143. 20 pp.

Minton, N. A., T. B. Hagler, and W. T. Brightwell. 1951. Nutrient-element deficiency symptoms of the rabbiteye blueberry. Proc. Amer. Soc. Hort. Sci. 58: 115-119.

Snedecor, G. W., and W. C. Cochran. 1967. Statistical Methods. Iowa State University Press, Ames. 593 pp.

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Response of the Spokane River Diatom Community to Primary Sewage Effluent[1]

Abstract

This study examines the effects of the primary sewage effluent from the City of Spokane, Washington, on the diatom community in the Spokane River. Both natural and artificial substrates were used at each of three sampling stations, one above and two below the sewage outfall, to determine the impact of the effluent on species composition, species diversity, and autotrophic index. Water chemistry samples were taken concurrently with diatom collections.

A total of 51 species in 18 genera of diatoms were identified. The flora was dominated by *Achnanthes* spp.; this genus accounted for 63.6 percent of the cells observed. Nine of the ten most abundant diatom taxa showed statistically significant changes in abundance below the sewage discharge. In each of these ten species there was a significant correlation between their numbers and orthophosphate or ammonia nitrogen concentrations.

In terms of individual species abundance, mean diversity indices, floristic similarities between sampling stations, and mean autotrophic indices, the diatom community at the last downstream station had begun to recover from the effects of organic pollution introduced via the sewage.

Introduction

The impact of the primary sewage effluent from the City of Spokane, Washington, on the water quality of the Spokane River has been studied in some detail (Cunningham and Pine, 1969; Bishop and Lee, 1972; and Soltero, Gasperino, and Graham, 1973, 1974). No attempt has been made, however, to show the effect(s) of this nutrient loading on the river flora.

The study area contains few aquatic macrophytes, and the permanent floral community is dominated by periphyton. Butcher (1932, 1940, 1947) and Patrick (1948) suggest that these sessile forms give the best indication of a lotic system's suitability for aquatic life. Since diatoms often dominate periphyton communities, they are used extensively to evaluate the impact of nutrient enrichment on rivers (Patrick, 1948, 1963; Holm and Hellerman, 1963; Bahls, 1971).

Analysis of community diversity is one method of studying the effect(s) of organic pollution on diatom communities (Patrick, Holm, and Wallace, 1954; Shobe, 1967). Unpolluted waters are usually characterized by a large number of species each with a relatively small population. Margalef (1951) suggested that an increase in available nutrients allows one or more species to take advantage of their innate capacity for population increase thereby decreasing his index of diversity.

Another approach to characterizing aquatic plant communities uses the autotrophic index (Weber and McFarland, 1969). This biomass to chlorophyll *a* ratio provides information as to the relative abundance of heterotrophs to autotrophs in a community.

[1]The work upon which this publication is based was supported in part by funds provided by the State of Washington Department of Ecology. Roland E. Pine served as Project Officer.

Initial investigation showed that periphyton in the study area was 75-95 percent diatoms. This information, plus the fact that diatoms are a relatively easy group to work with, led to their exclusive use in this study. The objectives of this investigation were: (1) to describe the species composition of the Spokane River diatom community; (2) to determine the effect of primary sewage effluent on this community by calculating diversity and autotrophic indices; and (3) to correlate the above information with selected physical and chemical parameters.

Description of the Study Area

The Spokane River is the effluent stream from Lake Coeur d'Alene in northern Idaho. The river flows in a westerly direction for 48 km before entering the City of Spokane, Washington. The average discharge of the river at Spokane for the period 1891 to 1973 was 194.3 m^3 sec^{-1} (U.S.G.S., 1973). Seasonal flows vary from about 42 m^3 sec^{-1} during low flow periods to spring maximums of about 540 m^3 sec^{-1}.

The Spokane sewage treatment plant is located just west of the city proper and discharges an average of 113,500 m^3 of primary treated sewage into the river daily. Three stations were established to monitor the effect of this effluent. Station A was 4.0 km above the outfall; stations B and C were 0.8 and 3.2 km, respectively, downstream from the treatment plant.

Methods and Materials

Water Quality

Water samples for chemical analysis were collected weekly from 15 July to 7 October 1974, and then monthly until termination of the study in December.

Temperature, pH, conductivity (at 25°C), and dissolved oxygen were measured using a Hydrolab ® Surveyor (model 6) on surface water samples. Similar samples were examined within 24 hours for turbidity, total alkalinity, sulfate, chloride, total hardness, calcium hardness, nitrate nitrogen, nitrite nitrogen, ammonia nitrogen, orthophosphate, and silica levels as described by the A.P.H.A. (1971).

Periphyton

Natural Substrates. Collections from natural substrates were made biweekly from 15 July to 7 October and continued at monthly intervals until termination of the study in December. Rocks are the primary natural substrate of the Spokane River, and several from each station were scraped with a pocket knife to give a composite collection. The diatoms in these collections were "cleaned" using the boiling nitric acid and potassium dichromate technique of Holm and Hellerman (1963). A solution of frustules was randomized and placed on a 22 x 50 mm cover slip, dried, and examined using a Nikon inverted phase contrast microscope. Successive fields of view were examined until 300 to 400 frustules had been identified and tabulated (Thomasson, 1925). These counts give the information necessary to establish species composition and percentage abundance. Community diversity was measured using the expression of Margalef (1951),

$$\bar{d} = \frac{M-1}{\ln N}$$

where $\bar{d}$ = diversity index, M = number of species in the sample, and N = number of individuals in the sample.

Artifical Substrates. Collections from artifical substrates were also made biweekly from 29 July to 7 October. Many artificial substrates have been used for periphyton accrual in other investigations (Cooke, 1956; Sladeckova, 1962). Plexiglass plates were chosen for this study because of their non-selective and durable nature (Peters, 1959). Each plate was attached to a 1.0 m steel rod driven into the river bottom at a point where current velocity was approximately 0.4 m sec^{-1}. The plates were oriented parallel to the surface at a depth of 0.3 m.

Scored lines on each plate delineated the area (0.021 m^2) from which quantitative samples were taken for biomass and chlorophyll *a* measurements. After a two-week accrual period the plates were transported in the dark to the laboratory and frozen. The periphyton was then scraped from the sampling area into a flask containing 90 percent acetone for phytopigment extraction. Chlorophyll *a* (mg m^{-2}) and organic biomass (mg m^{-2}) determinations were made following the procedures of Weber (1973). Biomass to chlorophyll *a* ratios (autotrophic indices) were then calculated for each plate.

Results

Water Quality

Mean orthophosphate concentrations increased five-fold below the sewage outfall, from 0.04 mg l^{-1} to 0.23 mg l^{-1} (Table 1). Mean nitrate nitrogen concentrations increased slightly at station B and continued to rise downstream. This increase, accompanied by a drop in ammonia nitrogen, indicated that much of the ammonia introduced via the

TABLE 1. Range and mean of the determined chemical and physical parameters for Spokane River stations A, B, and C.

	A	B	C
Temperature (°C)	5.5-19.0	5.9-18.8	5.9-18.9
	12.4	12.6	12.3
pH Range	7.87-8.45	7.78-8.09	7.86-8.31
Dissolved Oxygen	9.2-11.7	8.8-11.0	9.1-12.2
(mg l^{-1})	9.7	9.3	9.7
Conductivity	95 -172	104 -180	111 -187
(micromhos cm^{-1})	133	141	150
Turbidity (NTU)	1.0-3.3	1.3-2.6	0.9-2.0
	1.8	1.8	1.6
Total Alkalinity	46.4-97.2	51.2-98.4	54.7-99.9
(mgl^{-1} HCO_3)	71.7	74.6	80.2
SO_4^{-2} (mg l^{-1})	7.6-10.8	7.3-11.6	8.2-12.0
	9.3	9.4	9.8
Cl^- (mg l^{-1})	1.0-2.3	1.7-3.2	1.4-2.9
	1.8	2.3	2.1
Ca^{+2} (mgl^{-1})	9.6-22.9	11.2-24.4	12.8-26.5
	16.3	17.7	19.5
Mg^{+2} (mg l^{-1})	4.4-6.5	4.4-6.6	4.6-6.6
	5.4	5.3	5.6
NO_3-N (mg l^{-1})	0.28-0.57	0.36-0.51	0.45-0.72
	0.44	0.45	0.57
NO_2-N (mg l^{-1})	0.001-0.003	0.001-0.004	0.001-0.004
	0.002	0.002	0.002
NH_3-N (mg l^{-1})	0.02-0.15	0.11-0.33	0.06-0.32
	0.09	0.26	0.20
Ortho-PO_4^{-3} (mg l^{-1})	0.01-0.32	0.14-0.38	0.11-0.33
	0.04	0.23	0.19
SiO_2 (mg l^{-1})	8.0-14.6	7.6-14.0	8.2-14.0
	10.2	9.7	10.2

sewage was oxidized to nitrate by the time flow reached station C. Mean nitrite nitrogen levels were identical at all stations, and absolute values were low throughout the study.

Mean silica concentrations varied from 9.7 mg l^{-1} at station B to 10.2 mg l^{-1} at both A and C. All values were well above the 0.5 to 0.8 mg l^{-1} minimum set by Lund (1954) for the growth of certain diatoms. Total alkalinity (essentially all bicarbonate at the pH values observed), conductivity, sulfate, and calcium levels increased at both stations B and C.

The minimum water temperature recorded over the duration of the study was 5.5°C at station A on 16 December. The maximum was 19°C, also at station A, on 5 August. Mean dissolved oxygen concentrations were 9.7 mg l^{-1} at stations A and C, and 9.3 mg l^{-1} at station B. Although this decrease in D.O. at station B was not statistically significant, it may reflect increased biochemical oxygen demand from organic matter introduced via the sewage outfall.

Periphyton

Natural Substrates. A total of 51 species in 18 genera of diatoms were identified from natural substrate samplings. The 17 most frequently occurring diatom taxa are ranked according to occurrence in Table 2. Occurrence is the number of samples in which a given taxon occurred expressed as a percentage of the total number of samples examined. Taxa with less than 20 percent occurrence have been deleted. *Achnanthes minutissima* was the only diatom found in every sample, although three others, *Synedra rumpens, Nitzschia fonticola,* and *Achnanthes linearis* had occurrence values over 90 percent.

TABLE 2. Rank of the major diatom taxa of the Spokane River according to occurrence (%). Values based on collections from all stations on all dates.

Rank	Taxon	Occurrence (%)
1	**Achnanthes minutissima**	100.0
2	**Synedra rumpens**	96.7
	Nitzschia fonticola	96.7
4	**Achnanthes linearis**	93.3
5	**Navicula pelliculosa**	83.3
	Achnanthes deflexa	83.3
7	**Tabellaria fenestrata**	76.7
	Nitzschia amphibia	76.7
	Nitzschia palea	76.7
10	**Cymbella ventricosa**	70.0
11	**Fragilaria vaucheriae**	66.7
	Caloneis bacillum	66.7
	Gomphonema parvulum	66.7
14	**Melosira italica**	56.7
15	**Melosira varians**	40.0
16	**Cyclotella** spp.	26.7
	Synedra incisa	26.7

The most common diatom species are ranked according to abundance in Table 3. Abundance is the percentage contribution to the total cell count, and taxa with a value less than one percent have been omitted. *Achnanthes minutissima* and *Achnanthes linearis* were the most abundant taxa and together comprised over half of the total cell count. The 11 taxa listed account for nearly 97 percent of the cells identified at all stations throughout the study.

The top 11 taxa in Tables 2 and 3 are identical but not necessarily of the same rank. Two noteworthy examples are *Syndera rumpens* and *Achnanthes linearis*. *Synedra rumpens* occurred in 97.6 percent of the samples yet comprised only 3.5 percent of the total community. *Achnanthes linearis* ranked fourth in occurrence yet contributed 25 percent of the total cell count.

Table 4 lists the most common taxa along with their rank and mean abundance at each station and also shows whether the difference in abundance between two stations was significant. *Achnanthes minutissima, Achnanthes deflexa, Synedra rumpens, Tabellaria fenestrata, Fragillaria vaucheriae,* and *Cymbella ventricosa* all showed a pattern of highest mean abundance at station A, a decline at station B, and recovery at station C. *Achnanthes linearis* and *Navicula pelliculosa* showed a pattern of lowest mean abundance at station A, highest at station B, and a decline at station C. *Nitzschia fonticola* and *Nitzschia palea* showed a pattern of lowest mean abundance at station A, an increase at station B, and the highest mean abundance at station C.

Similarities between sampling stations were determined using the formula of Whittaker and Fairbanks (1958):

$$PS_c = 100 - 0.5\Sigma|X - Y|$$

where PS_c is the "percentage similarity of community samples" and X and Y are, for a given taxa, the mean abundance at station x and y which that species contributes. This index was calculated for the three possible station pairs. Floristically, the two most similar stations were the downstream stations with a percentage similarity of

TABLE 3. Rank of the major diatom taxa of the Spokane River according to abundance (%). Values based on collections from all stations on all dates.

Rank	Taxon	Abundance (%)
1	**Achnanthes minutissima**	27.2
2	**Achnanthes linearis**	25.0
3	**Achnanthes deflexa**	11.4
4	**Nitzschia fonticola**	10.1
5	**Navicula pelliculosa**	6.8
6	**Nitzschia palea**	5.9
7	**Synedra rumpens**	3.5
8	**Tabellaria fenestrata**	3.3
9	**Fragilaria vaucheriae**	1.3
	Cymbella ventricosa	1.3
11	**Nitzschia amphibia**	1.0

TABLE 4. The rank and mean abundance (%) at each station of the major diatom taxa. The * indicates that the difference in abundance between two stations is significant ($P = 0.05$).

Taxon	A		B		C		Significant Differences		
	Rank	(%)	Rank	(%)	Rank	(%)	A vs B	B vs C	A vs C
Achnanthes minutissima	1	34.6	2	16.5	1	30.4	*	*	-
Achnanthes linearis	7	2.1	1	47.2	2	25.8	*	*	*
Achnanthes deflexa	2	32.7	9	0.4	10	0.9	*	-	*
Nitzschia fonticola	5	5.2	5	7.3	3	17.9	-	*	*
Navicula pelliculosa	11	0.6	3	15.5	5	4.3	*	*	*
Nitzschia palea	9	1.6	4	7.4	4	8.8	-	-	*
Synedra rumpens	3	7.3	8	0.7	6	2.4	*	*	*
Tabellaria fenestrata	4	6.0	7	1.4	6	2.4	-	-	-
Fragilaria vaucheriae	6	3.1	14	0.0	12	0.7	*	*	*
Cymbella ventricosa	8	1.8	9	0.4	8	1.7	*	-	-

66.7. The least similar pair was A and B, with a value of 31.8 percent. Stations A and C were 51.1 percent similar.

The abundance of the ten most important diatom correlated significantly with at least one of the major nutrients (Table 5). *Achnanthes linearis* and *Navicula pelliculosa* had significant positive correlations with both phosphate and ammonia nitrogen. Three taxa, *Achnanthes deflexa, Snyedra rumpens,* and *Cymbella ventricosa* had significant negative correlations with both phosphate and ammonia nitrogen. *Achnanthes minutissima* had a significant negative correlation with ammonia nitrogen; its correlation with phosphate was negative but not significant.

Nitzschia fonticola had significant positive correlations with all three forms of inorganic nitrogen. Its strongest correlation was with nitrate nitrogen, which was the only major nutrient that increased at station C over its value at station B. This finding may explain why *N. fonticola* did not exhibit an abundance value at station C intermediate to that of stations A and B as did most of the other taxa.

Diversity indices ranged from a low of 1.18 at station A on 21 October to a high of 3.25 at station C on 16 December. Mean diatom diversity was 2.30 at station A, 1.82 at station B, and 2.38 at station C. Mean diversity values at stations A and C were both significantly different from station B. Correlations between diatom diversity and orthophosphate and ammonia nitrogen concentrations were negative but not significant.

Artificial Substrates. The results of artificial substrate samplings are given in Table 6. Mean chlorophyll *a* concentrations decreased downstream from the sewage effluent while mean biomass accural was essentially the same at stations A and B but dropped at station C. The mean autotrophic index was 203 at station A but increased significantly to 1005 at station B. At station C it averaged 649. Correlation coefficients between the autotrophic index and orthophosphate and ammonia nitrogen concentrations were positive but not significant.

Discussion

The City of Sopkane's primary sewage effluent had a marked effect on the relative abundance of individual diatom species. Each of the ten most abundant taxa was found

TABLE 5. Simple correlation coefficients (r) between nutrient concentrations and abundance of the major diatom taxa for all stations over all dates.

Taxon	PO_4^{-3}	NH_3-N	NO_3^--N
Achnanthes minutissima	-0.312	-0.424*	0.214
Achnanthes linearis	0.715***	0.430*	0.112
Achnanthes deflexa	-0.647***	-0.488**	-0.415*
Nitzschia fonticola	0.348	0.427*	0.515**
Navicula pelliculosa	0.599***	0.608***	-0.184
Nitzschia palea	0.343	0.598***	0.054
Synedra rumpens	-0.625***	-0.580**	0.109
Tabellaria fenestrata	-0.383*	-0.134	-0.288
Fragilaria vaucheriae	-0.463*	-0.294	-0.020
Cymbella ventricosa	-0.488**	-0.609***	0.112

* P = 0.05
** P = 0.01
*** P = 0.001

at all three stations, but there was a significant difference in abundance values above and below the sewage outfall for nine of these species. The only exception was *Tabellaria fenestrata* which did not exhibit statistically significant variations; however, its abundance at station A was higher than at B in every sample.

TABLE 6. Actual and mean station values for chlorophyll a (mg m^{-2}), biomass (mg m^{-2}) and autotrophic index.

Accrual Period	A			B			C		
	chl a	Biomass	A.I.	chl a	Biomass	A.I.	chl a	Biomass	A.I.
7/15-7/29	4.76	1074	226	0.09	156	1714	5.09	1076	211
7/29-8/12	22.18	5218	235	3.95	1587	402	9.57	1611	168
8/12-8/26	6.66	1887	283	17.35	6156	355	1.01	911	906
8/26-9/9	9.94	2084	210	10.92	3860	354	2.21	1279	579
9/9-9/23	9.90	1652	167	0.09	170	1971	3.29	1647	501
9/23-10/7	1.06	102	96	0.05	58	1231	1.39	2121	1526
Mean	9.08	2003	203	5.41	1998	1005	3.76	1441	649

Patrick (1964) concluded that increases in the percentage of the community contributed by the dominant species and decreases in the total number of species are reliable indicators of the general pollution load of a river. There were 30 percent fewer species identified at station B than at station A or C and the dominant species contributed 34.6, 47.2, and 30.4 percent of the community at stations A, B, and C, respectively. This trend is also illustrated by the depression of the mean diversity index from 2.39 at station A to 1.82 at B and its subsequent recovery to 2.38 at station C.

Eight of the ten most common taxa exhibited abundance values at station C intermediate to those at A and B. The two exceptions were *Nitzschia fonticola* and *Nitzschia palea.* Cholnoky (1960) reported that the abundance of *Nitzschia* spp. in a diatom community was proportional to the levels of dissolved nitrogen compounds. Mean total inorganic nitrogen concentrations were 0.53, 0.71, and 0.77 mg l^{-1}. *Nitzschia fonticola* and *N. palea* together comprised 6.8, 14.7, and 26.7 percent of the total community at stations A, B, and C, respectively. These statistics help explain why the mean abundance of these two diatoms did not exhibit intermediate values at station C and may also indicate that the other diatom taxa are responding to some environmental parameter other than nitrogen concentrations.

Seven of the ten most abundant diatom taxa correlated significantly with orthophosphate. Of the three that did not, two were the species of *Nitzschia* just mentioned. The third, *Achnanthes minutissima*, has been shown to be extremely sensitive to changes in dissolved oxygen levels (Cholnoky, 1968). Mean dissolved oxygen concentrations were 9.7 mg l^{-1} at stations A and C, but dropped to 9.3 mg l^{-1} at station B. Soltero *et al.* (1973, 1974) also showed decreased oxygen levels below the sewage outfall in 1972 and 1973. *Achnanthes minutissima* had mean abundance values of 34.6, 16.5, and 30.4 percent at stations A, B, and C, respectively.

Floristically, station A was more similar to station C than to station B; B and C were more similar than A and C. Thus, on the basis of percentage similarity between community samples, station C was intermediate to the other sampling sites.

The mean autotrophic index increased from 203 at station A to 1005 at station B. Weber and McFarland (1969) reported values of 177 above and 1019 below the Cincinnati, Ohio municipal sewage discharge to the Ohio River. Bahls (1971) reported

nearly a four-fold increase in autotrophic index for the East Gallatin River below the City of Bozeman, Montana, sewage treatment plant. The mean index value of 649 at station C was not significantly different from either station A or B, possibly indicating that it was intermediate to these two stations.

Therefore, in terms of abundance of individual species, mean diversity indices, percentage similarity between stations, and mean autotrophic indices, station C appears to be a "recovery" station.

Literature Cited

American Public Health Association. 1971. Standard Methods for the Examination of Water and Wastewater. 13th ed. A.P.H.A., New York. 874 pp.

Bahls, L. L. 1971. Ecology of the Diatom Community of the Upper East Gallatin River, Montana, with *In situ* Experiments on the Effect of Current Velocity on Features of the *Aufwuchs*. Montana State University, Bozeman, Ph.D. thesis. 145 pp.

Bishop, R. A., and R. A. Lee. 1972. Spokane River Water Quality Study. D.O.E. Technical Report No. 72-001. 72 pp.

Butcher, R. W. 1932. Studies in the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river bed. Ann. Bot., 46: 813-861.

————. 1940. Studies in the ecology of rivers. IV. Observations on the growth and distribution of the sessile algae in the River Hull, Yorkshire. Jour. Ecol., 28: 210-223.

————. 1947. Studies in the ecology of rivers. VII. The algae of organically enriched waters. Jour. Ecol., 35. 186-191.

Cholnoky, B. J. 1960. *In* A. D. Harrison, P. Keller, and D. Dimovic. Ecological studies on Olifantsvlei, near Johannesburg: with notes on the diatoms by B. J. Cholnoky. Hydrobiol., 15: 89-134.

————. 1968. Die Okologie de Diatomeen in Binnengewassern. J. Cramer, Lehre. 699 pp.

Cooke, W. B. 1956. Colonization of artificial bare areas by microorganisms. Bot. Rev., 22: 613-638.

Cunningham, R. K., and R. E. Pine. 1969. Preliminary Investigation of the Low Dissolved Oxygen Concentrations that Exist in Long Lake Located near Spokane, Washington. W.W.P.C.C. Technical Report No. 69-1. 24 pp.

Hohn, M. H., and J. Hellerman. 1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. Trans. Amer. Microsc. Soc., 82: 250-329.

Lund, J. W. G. 1954. The seasonal cycle of the plankton diatom *Melosira italica* (Ehr.) Kutz subsp. *subarctica* O. Mull. Jour. Ecol., 42: 151-179.

Margalef, R. 1951. Diversidad de especies en las communidades naturales. P. Inst. Biol., Apl. 9: 5-27.

Patrick, R. 1948. Factors effecting the distribution of diatoms. Bot. Rev., 14: 473-524.

————. 1963. The structure of diatom communities under varying ecological conditions. Ann. N.Y. Acad. Sci., 108: 259-365.

————. 1964. A discussion of natural and abnormal diatom communities. *In* D. F. Jackson, ed., Algae and Man, pp. 185-204, Plenum Press, New York.

————, M. H. Hohn, and J. H. Wallace. 1954. A new method for determining the pattern of the diatom flora. Bot. Nat. Acad. Nat. Sci., 259: 1-12.

Peters, J. C. 1959. An Evaluation of the Use of Artificial Substrates for Determining Primary Production in Flowing Water. Michigan State University, East Lansing, M.S. thesis. 106 pp.

Shobe, W. R. 1967. A Study of the Diatom Communities in a Hardwater Stream. Iowa State University of Science and Technology, Ames, Ph.D. thesis. 111 pp.

Sladeckova, A. 1962. Limnological investigation methods for the periphyton ("Aufwuchs") community. Bot. Rev., 28: 286-350.

Soltero, R. A., A. F. Gasperino, and W. G. Graham. 1973. An Investigation of the Cause and Effect of Eutrophication in Long Lake, Washington. O.W.R.R. Project 143-34-10E-3996-5501. Final Progress Report. 86 pp.

————, ————, and ————. 1974. Further Investigations as to the Cause and Effect of Eutrophication in Long Lake, Washington. D.O.E. Project 74-025A. Completion Report. 85 pp.

Thomasson, K. 1925. Methoden zur Untersuchung der Mikrophyten der limnischen Litoral—und Profundalzone. Abderhalden's Handbuch der biologischen Arbeitsmethoden, Abt. IX, Teil 2, 1. Berlin.

U.S. Geological Survey. 1973. Water Resources Data for Washington. Part I. Water surface records. 430 pp.

Weber, C. I. 1973. Biological Field and Laboratory Methods for Measuring the quality of Surface Waters and Effluents. Environmental Protection Agency, National Environmental Research Center, Cincinnati, Ohio. 126 pp.

————, and B. H. McFarland. 1969. Periphyton Biomass—Chlorophyll Ratio as an Index of Water Quality. Unpub. report. Anal. Qual. Cont. Lab., F.W.P.C.A., U.S.D.I., Cincinnati, Ohio. 19 pp.
Whittaker, R. H., and C. W. Fairbanks. 1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecol., 39: 46-65.

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Variation within the Sagebrush Vegetation of Grand Teton National Park, Wyoming[1]

Abstract

The distribution, species composition, and physical soil characteristics are described for four different sagebrush communities in Grand Teton National Park, Wyoming. The communities are characterized, respectively, by *Artemisia arbuscula; A. tridentata; A. tridentata* and *A. arbuscula;* and *A. tridentata* and *Purshia tridentata.* The community dominated by *A. arbuscula* is restricted to the west side of the Snake River, close to the Teton Range where the soils are more coarsely textured. The most widespread community is a patchy mosaic of *A. arbuscula* and *A. tridentata. Purshia* was observed only in the southern portion of the study area, but none of the measured soil features were strongly correlated with its distribution. *Koeleria cristata* and several annuals (*Collinsia parviflora, Collomia linearis, Gayophytum nuttallii*) were more abundant on the coarse-textured soils; *Festuca idahoensis* was more common on the finer textured soils. The current distribution of the communities may be related to past geological events.

Introduction

The vegetation of the Snake River glacial outwash plains in Grand Teton National Park is characterized generally by the abundance of big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* Rydb.) and locally by mixtures of big sagebrush and low sagebrush (*A. arbuscula* Nutt.) or big sagebrush and bitterbrush (*Purshia tridentata* (Pursh) D. C.). As Figure 1 shows, big sagebrush occurs to the near exclusion of the other two shrub species east of the Snake River, except in the vicinity of Blacktail Butte where bitterbrush is intermixed, while west of the river low sagebrush is commonly intermixed in a mosaic manner with big sagebrush (Fig. 2). Near Jenny Lake there are stands of low sagebrush with very little or no big sagebrush and bitterbrush. The distribution of these four community types is of special interest ecologically because the relatively flat glacial outwash plains in the Park present what appears superficially to be a homogeneous environment (Houston, 1967). In this report we present the results of a study on the correlation of soil characteristics with the distribution of the species that commonly occur in the sagebrush vegetation.

Several investigators have observed that soil structure and texture are correlated with big sagebrush, low sagebrush, and bitterbrush distribution. Driscoll (1964) found that bitterbrush in Oregon occurred on coarse textured, stony soils while big sagebrush occurred on finer textured, non-stony soils; and that low sagebrush and big sagebrush appear to be segregated in some locales by the depth to a relatively impermeable soil stratum. Fosberg (1963), working in southern Idaho, found the depth to either a clay B horizon or bedrock was 33 cm or less for soils supporting low sagebrush, but

[1]Project No. 169 of the Jackson Hole Biological Research Station.

deeper for soils with big sagebrush. Similarly, Summerfield and Peterson (1971) found that low sagebrush soils in northwest Nevada had a prismatic and blocky structured clay horizon at 8 to 30 cm from the surface, whereas all soils supporting big sagebrush had the compound prismatic blocky structure at greater depths (30-53 cm). Hironaka (1963) found that low sagebrush occurred primarily on poorly aerated soils in Idaho, the poor aeration being caused by a restrictive layer in the soil profile which

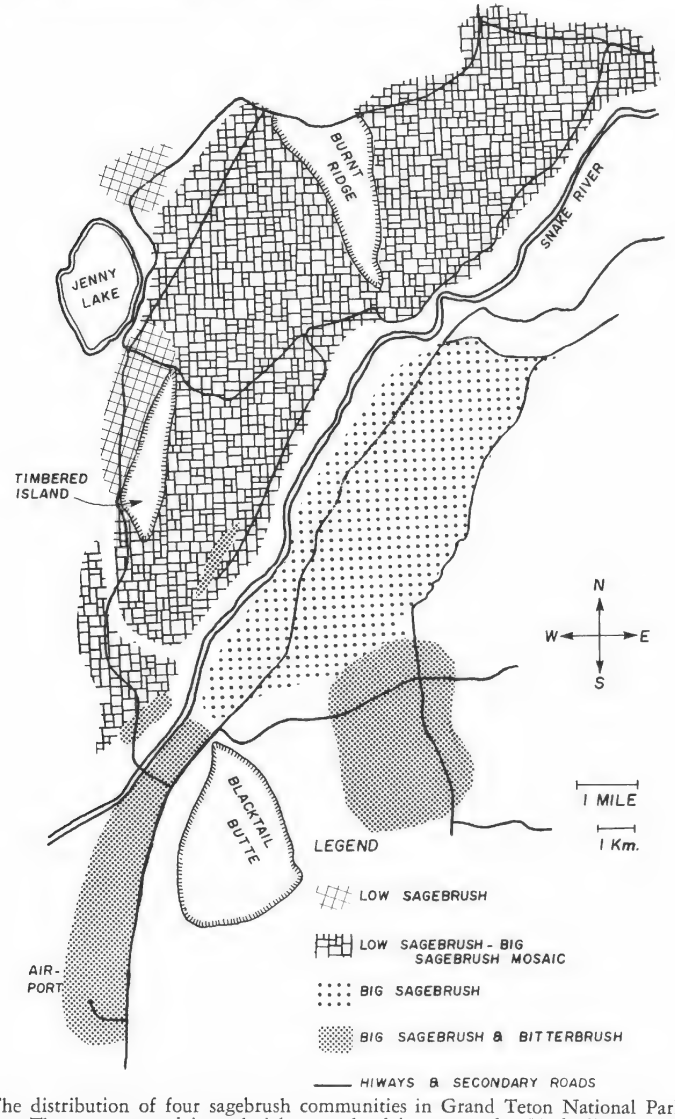

Figure 1. The distribution of four sagebrush communities in Grand Teton National Park, Wyoming. The area mapped is a glacial outwash plain, except for Blacktail Butte, two glacial moraines (Timbered Island and Burnt Ridge), and the area northeast of Burnt Ridge which was covered by ice during the Pinedale glaciation (Love and Reed, 1968).

Figure 2. The mixed sagebrush community, showing the mosaic of patches dominated by either big sagebrush or low sagebrush (foreground).

caused water to stand on the surface for several weeks in late winter. Whether big sagebrush is excluded by a restrictive layer because of poor aeration or some other influence is still an unresolved question.

Although the studies reviewed above found low sagebrush correlated with a relatively shallow restrictive layer in the soil profile, this restrictive layer was not found in the glacial outwash of Grand Teton National Park. Soil pits were dug to 80 cm in 31 stands, and no restrictive layers or evidence of a B horizon were observed. Fosberg (1963) found that soil texture was correlated with the distribution of low and big sagebrush on Idaho soils that lacked a clay B horizon, observing that low sagebrush occurred on soils with 30 percent or more gravels throughout the profile; big sagebrush soils contained less than 30 percent gravels. One of our objectives was to determine if Fosberg's results were applicable to Grand Teton National Park.

The Study Area

The sagebrush community of Grand Teton National Park lies at an elevation of 1947 to 2114 m, and covers an area of about 168 sq km. The substrate is predominantly an outwash plain formed after the Pinedale glaciation, which occurred 9000 to 15,000 years ago (Love and Reed, 1968). Reed (1952), Beetle (1961), Oswald (1966), and Houston (1967) have described various aspects of the vegetation in the Park, but none has reported on the variations within the sagebrush communities.

The only available climatic data for the Park are from the Moran weather station, located at the Jackson Lake Dam (43°51′ lat. N., 110°35′ long. W.) at an elevation

of 2060 m. This station is approximately 4.0 km north-northeast of the northernmost stand we studied. The average annual precipitation at the Moran station is 54.1 cm, about 22 percent (12.2 cm) of which falls in the 13-week period from May 24 to August 23. Snow is the predominant form of precipitation, with only light showers occurring during the dry mid-summer period. July has the highest mean temperature, 14.5°C, with 32°C and −5°C being the maximum and minimum temperatures observed, respectively, during July (Becker and Alyea, 1964).

Methods

Thirty-one stands were located objectively by placing points on a map of the Park in such a manner that all types of sagebrush vegetation that occur on the glacial outwash plains were represented. Each stand was 100 x 200 feet in size (30.3 x 60.6 m) and appeared homogeneous in species composition and topography. Seven were dominated by low sagebrush, seventeen by big sagebrush, and seven by big sagebrush and bitterbrush. Three stands dominated by big sagebrush were located on alluvium, thereby affording the opportunity to observe how the glacial outwash stands were different. Sabinske (1972) shows the location of each stand.

The herbaceous flora at each stand was sampled for frequency with 40 one-square-foot quadrats (0.093 m^2) located in a random manner. Species found in the stand but not in the quadrat were recorded as being present in the stand. The nomenclature is that of Shaw (1976).

The quadrat data were obtained from 24 June to 11 July in 1970 and from 26 June to 7 July in 1971. This period in late June and early July coincides with the blooming of most species. Some common species were not sampled, however, because they bloomed and decayed before the sampling period, for example, *Ranunculus jovis* A. Nels. and *Claytonia lanceolata* Pursh. *Machaeranthera canescens* Pursh, an annual, was counted in the form of seedlings, of which there were large numbers.

The only major identification problem occurred between *Sitanion hystrix* and *Agropyron dasystachyum,* two grass species which we did not learn to distinguish without flowers until after 13 stands had been sampled. The data for these species were not used, therefore, in the data analysis.

Shrub cover in each stand was sampled by species, using the line intercept method. Ten 100 foot (30.3 m) line transects were placed parallel to the short axis of the stand at 6 m intervals.

Soil samples were obtained from three or four randomly located pits in each stand. One sample was taken from 0 to 10 cm and another from 10 to 20 cm. Enough soil was screened from each layer so that the portion with particles less than 2 mm in diameter weighed a minimum of 1 kg. The weight of the portion greater than 2 mm was recorded and then discarded. The <2 mm portion of each sample was analyzed for organic matter content, using the wet combustion method of Walkley-Black (Black *et al.,* 1965). The sample was then analyzed for texture, using the Bouyoucos hydrometer method (Bouyoucos, 1927).

Data analysis was facilitated by principal component analysis, using a weighted similarity coefficient described by Orloci (1966). A similarity matrix was calculated for the 31 stands using frequency and cover data for 75 species (Sabinske, 1972); this matrix served as the basis for a two-dimensional ordination of the stands, on

which the distance between any two stands is inversely proportional to the degree of similarity of the stands as estimated with the coefficient. The ordination served as a tool for studying species composition gradients in relation to soil characteristics.

Results

Between 50 and 66 species were found in each of the four major community types (Table 1). The low sagebrush stands had a total of 57 species, of which one, *Poa interior,* was not found in any other stand. The big sagebrush-bitterbrush stands had a total of 65 species, with six of these being restricted to this community, namely, *Amelanchier alnifolia, Campanula rotundifolia, Frasera speciosa, Geranium viscosissimum, Potentilla arguta,* and *Wyethia amplexicaulis.* The big sagebrush stands on glacial outwash had 66 species and the three big sagebrush stands on alluvium had 51 species.

TABLE 1. The percentage of stands in which species occurred (% Presence) for the four major sagebrush communities in Grand Teton National Park. The number of stands studied for each community type is shown in parentheses. Species that occurred in only one stand are not included.

Species	Big Sagebrush Community (15)	Low Sagebrush Community (6)	Mixed Sagebrush Community (6)	Big Sagebrush Bitterbrush Community (5)
Artemisia arbuscula Nutt.	0	100	100	0
Artemisia tridentata Nutt. ssp. **vaseyana** Rydb.	100	33	100	100
Purshia tridentata (Pursh) DC.	13	0	40	100
Achillea millefolium L. ssp. **lanulosa** (Nutt.) Piper	33	0	0	60
Agropyron dasystachyum (Hook.) Scribn.	27	50	60	100
Agoseris glauca (Pursh) Raf.	47	0	0	0
Antennaria dimorpha (Nutt.) Torr. & Gray	47	0	0	20
Antennaria sp.	93	33	60	60
Arabis drummondii A. Gray	87	0	100	100
Arabis holboellii Hornem	73	33	100	20
Arenaria congesta Nutt.	40	66	80	0
Astragalus miser Dougl. var. **hylophilus** (Rydb.) Barneby	33	0	0	0
Balsamorhiza sagittata (Pursh) Nutt.	47	0	100	80
Berberis repens Lindl.	7	0	0	20
Carex sp.	100	66	60	80
Castilleja pilosa (S. Wats.) Rydb.	93	100	80	60
Chrysothamnus nauseosus (Pall.) Britt.	33	0	0	0
Collinsia parviflora Dougl.	87	100	100	100
Collomia linearis Nutt.	87	100	100	100
Commandra umbellata (L.) Nutt. var. **pallida** (DC.) Jones	73	17	80	80
Crepis acuminata Nutt.	60	17	20	60

TABLE 1. (Continued)

Danthonia unispicata (Thurb.) Munro.	7	50	40	0
Delphinium nuttallianum Pritz.	93	66	100	60
Dodecatheon conjugens Greene	53	33	80	0
Draba nemorosa L.	13	0	0	20
Erigeron ochroleucus Nutt.	73	50	60	40
Erigeron pumilus Nutt. ssp. **intermedius** Cronq.	27	33	40	0
Eriogonum umbellatum Torr. var. **subalpinum** (Greene) M. E. Jones	100	100	100	100
Eriophyllum lanatum (Pursh) Forbes var. **integrifolium** (Hook.) Smiley	7	0	60	0
Festuca idahoensis Elmer	93	83	40	100
Fritillaria atropurpurea Nutt.	20	0	0	40
Fritillaria pudica (Pursh) Spreng.	27	83	100	60
Galium bifolium S. Wats.	20	83	100	20
Gayophytum nuttallii Torr. & Gray	80	100	80	60
Geranium viscosissimum F. & M.	0	0	0	40
Geum triflorum Pursh var. **ciliatum** (Pursh) Fassett	20	0	0	0
Gilia aggregata (Pursh) Spreng.	33	0	40	60
Gymnosteris parvula Heller	27	50	40	60
Helianthella uniflora (Nutt.) Torr. & Gray	13	0	0	60
Koeleria cristata (L.)	100	100	100	100
Linanthus septentrionalis Mason	80	100	100	40
Linum perenne L. var. **lewisii** (Pursh) Eat. & Wright	7	0	0	20
Lithophragma bulbifera Rydb.	87	100	100	80
Lithospermum ruderale Dougl.	33	0	0	60
Lomatium ambignum (Nutt.) Coult. & Rose	20	0	20	0
Lomatium triternatum (Pursh) Coult. & Rose	73	66	40	60
Lupinus sericeus Pursh	87	100	100	100
Machaeranthera canescens (Pursh) Gray	66	83	80	60
Melica spectabilis Scribn.	47	83	100	40
Microseris nutans (Geyer) Schultz-Bip.	100	100	100	80
Mimulus floribundus Dougl.	13	17	20	0
Nemophila brevifolia A. Gray	20	0	60	40
Orobanche fasiculata Nutt.	0	17	20	0
Perideridia sp.	53	50	80	20
Phleum pratense L.	7	0	0	20
Phlox hoodii Rich.	20	0	0	0
Phlox longifolia Nutt.	73	0	20	100
Poa interior Rydb.	0	33	0	0
Poa pratensis L.	33	0	20	100
Poa sandbergii Vasey	60	50	60	60

TABLE 1. (Continued)

Polygonum kelloggii Greene	93	83	100	80
Potentilla arguta Pursh ssp. **convallaria** (Rydb.) Th. Wolf	0	0	0	40
Rumex paucifolius Nutt.	7	83	40	0
Sedum stenopetalum Pursh	33	100	100	40
Senecio integerrimus Nutt.	80	83	60	80
Sitanion hystrix (Nutt.) J. G. Smith	40	66	40	0
Stipa lettermanii Vasey	27	0	0	0
Symphoricarpos oreophilus A. Gray var. **utahensis** (Rydb.) A. Nels.	33	0	0	20
Taraxacum officinale Weber	87	66	40	100
Tragopogon porrifolius L.	13	0	0	40
Viola sp.	40	33	60	60
Zigadenus paniculatus (Nutt.) S. Wats.	40	0	20	0

The stands dominated by low sagebrush (*Artemisia arbuscula*) were located on the west side of the Snake River (Fig. 1), the low sage being most abundant where there was little or no big sage. The minimum cover for low sagebrush was 11.2 percent. There were nine species which reached their peak abundance in stands dominated by low sagebrush—*Sedum stenopetalum, Lithophragma bulbifera, Melica spectabilis, Koeleria cristata, Collomia linearis, Collinsia parviflora, Polygonum kelloggii, Gayophytum nuttallii,* and *Linanthus septentrionalis.*

Big sagebrush was the most widely distributed of the shrubs, having its highest cover in the stands on the east side of the Snake River (15-26 percent). Species which had distribution centers similar to big sagebrush were *Eriogonum umbellatum, Taraxacum officinale, Crepis acuminata, Agoseris glauca, Phlox longifolia,* and *Festuca idahoensis.* Bitterbrush is a codominant with big sagebrush toward the south end of the study area. Several species reached their peak abundance with bitterbrush, including *Helianthella uniflora, Tragopogon porrifolius, Poa pratensis, Lithospermum ruderale,* and *Achillea millefolium.* The mixed sagebrush community occurs as a mosaic of patches (commonly 3-6 m across) dominated by either big or low sagebrush, and is restricted to the west side of the Snake River (Fig. 1).

The soil data were summarized by community type also (Table 2), with one trend being most apparent—the low sagebrush community has a larger percentage ($x = 62$ percent) of coarse material (> 2 mm) at 10-20 cm than the stands dominated by big sagebrush ($x = 43$ percent). This trend was substantiated further by the calculation of a correlation coefficient. As the amount of soil material > 2 mm increases at 10-20 cm depth, the percent cover of low sagebrush increased ($r = .53$, p 99 percent) and the cover of big sagebrush decreased ($r = .42$, p 95 percent). Stands with bitterbrush are intermediate in soil coarseness, on the average, and do not have a significant correlation with the percentage of material > 2 mm. Bitterbrush was positively correlated with the amount of sand (1-2 mm) in the soil ($r = .42$, p 95 percent), while the two sagebrush species had no correlation with this feature. *Koeleria, Collinsia, Collomia,* and *Gayophytum* were more abundant on the more coarsely textured

soils, being positively associated with low sagebrush. *Festuca idahoensis* occurred more frequently with big sagebrush on the finer textured soils.

The first component (axis) of the principal component analysis accounted for 36 percent of the variance and separated the communities dominated by low sagebrush from those dominated by big sagebrush. The second component accounted for only 13 percent of the variance and the third for 9 percent. The distribution on the ordination of most species is presented in Sabinske (1972).

TABLE 2. Soil characteristics at two depths (cm) of four sagebrush communities in Grand Teton National Park. The values are means, with the range in parentheses.[a]

Soil Feature	Big Sagebrush Community		Low Sagebrush Community		Mixed Sagebrush Community		Big Sagebrush-Bitterbrush Community	
	0-10	10-20	0-10	10-20	0-10	10-20	0-10	10-20
Texture								
% Clay	29 (21-39)	29 (20-40)	26 (25-28)	25 (23-27)	26 (25-30)	27 (24-31)	30 (23-41)	30 (28-41)
% Silt	39 (32-51)	39 (32-48)	39 (33-43)	40 (35-43)	40 (34-45)	39 (34-45)	34 (23-40)	33 (25-38)
% Sand	31 (18-45)	32 (20-43)	35 (29-43)	35 (33-41)	33 (26-40)	34 (25-40)	37 (19-48)	37 (24-47)
% > 2mm	41 (12-61)	43[a] (19-67)	55 (53-62)	62[a] (55-68)	55 (51-62)	64 (47-82)	45 (22-59)	41 (11-62)
Organic Matter (%)	5.3 (3.7-6.8)	3.7 (2.2-4.9)	5.3 (4.4-6.3)	4.0 (3.5-4.6)	6.4 (5.6-7.0)	4.4 (3.9-4.8)	5.0 (3.5-6.1)	4.0 (2.5-5.2)

[a]Significant differences could not be detected with a confidence level greater than 65 percent, but a correlation analysis (see text) suggested that the amount of coarse material is higher in the low sagebrush community.

Discussion

Our results are similar in some respects to those of Fosberg (1963), who found that low sagebrush in southern Idaho characteristically has coarser soils. Unlike Fosberg, we could not identify a soil texture boundary for separating the two community types. Although low sagebrush appears to be limited by soil texture, big sagebrush was found on coarse soils as well as on those that are fine textured.

As noted previously, several investigators have found low sagebrush restricted to soils with a dense or impermeable horizon in the soil profile, a feature that we did not observe on the outwash plains of Grand Teton National Park. Coarse-textured soils and soils with an impermeable horizon have one feature in common, however—they provide a very dry habitat for plant growth where summer rainfall is minimal, such as in the Park. We suggest that low sagebrush is restricted to the more coarse-textured soils and/or shallow soils because it is more drought tolerant than big sagebrush, and that it does not occur on the finer textured soils because it cannot compete there with big sagebrush and other associated species. The low sagebrush-big sagebrush mosaic that is common west of the Snake River (Figs. 1 and 2) would provide an ideal location to test this hypothesis.

With regard to the bitterbrush stands, no soil textural trend was observed. Driscoll (1964) found soil texture useful for separating big sagebrush from bitterbrush in Oregon, but the two species are codominants in the southern part of Grand Teton

National Park. The unique feature of the southern part of the Park that allows the abundance of bitterbrush is not clear at this time, although it could be related to the percentage of sand and silt at 10 to 20 cm.

It is intriguing to speculate on why the more coarse soils and low sagebrush are restricted to the west side of the Snake River (Fig. 1). Although the glacial outwash on both sides of the River is of the same age (Love and Reed, 1968), the origin of the outwash material on the east side is thought to be predominately from the Washakie and Absaroka Ranges to the east and northeast,[2] whereas that on the west side is from the granitic Teton Range to the west (J. D. Love, pers. comm.). Ice masses from the two areas are believed to have merged just north of Burnt Ridge (Fig. 1), from where the outwash moved south. Although some blending of the two sets of parent material no doubt occurred, differences between the eastern and western sides of the valley probably persist to this day. A larger source of clay was available in the ranges to the east, and we found that finer textured soils predominate east of the Snake River.

The distribution of bitterbrush also may be related to the geologic history of the area. The stand east of Blacktail Butte (Fig. 1) occurs on a large alluvial fan at the mouth of Ditch Creek that is nearly the same age as the glacial outwash, but which is of different rock type and origin. The fan consists largely of locally derived sandstone fragments and clays brought westward about 8 km. The bitterbrush between Blacktail Butte and the airport occurs on glacial outwash that is a composite of rock types from the mountains to the east and west (J. D. Love, pers. comm.).

Thus, the distribution of the sagebrush communities in Grand Teton National Park appears to be related to geologic events that occurred more than 8000 years ago. Further study is necessary to verify this possibility, but no other explanation seems as plausible for the distribution of the four community types in an area that superficially appears to be very homogeneous.

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Literature Cited

Becker, C. F., and J. D. Alyea. 1964. Temperature Probabilities in Wyoming. Wyo. Agr. Exp. Sta. Bull. 415. 157 pp.

Beetle, A. D. 1961. Range survey in Teton County, Wyoming. Part I. Ecology of range resources. Wyo. Agr. Exp. Sta. Bull. 376: 1-42.

Black, C. A, D. D. Evans, J. L. White, L. E. Ensminger, F. E. Clark, and R. C. Dinaur. 1965. Methods of Soil Analysis. Part 2: Chemical and microbiological properties. Agron. Monog. No. 9, Part 2, American Society of Agronomy, Inc. 802 pp.

[2]Quartzite boulders originate from the Pinyon Peak Highlands, carbonate rocks from the Washakie Range, coarse volcanic debris from the Absaroka Range, and clays from the Cretaceous and Tertiary shales and claystones within 16 km to the northeast (J. D. Love, pers. comm.).

Bouyoucos, G. J. 1927. The hydrometer method for the mechanical analysis of soils. Soil Sci. 23: 343-353.
Driscoll, R. S. 1964. A relict area in the central Oregon juniper zone. Ecology 45: 345-353.
Fosberg, M. A. 1963. Genesis of Some Soils associated with Low and Big Sagebrush Complexes in the Brown, Chestnut, and Chernozem prairie zones in southcentral and southwestern Idaho. Univ. Wisconsin, Madison, Ph.D. thesis. 332 pp.
Hironaka, M. 1963. Plant-Environment Relations of Major Species in Sagebrush-Grass Vegetation of Southern Idaho. Univ. of Wisconsin, Madison, Ph.D. thesis. 138 pp.
Houston, Douglas B. 1967. The Shiras Moose in Jackson Hole, Wyoming. (Department of Zoology and Physiology), Univ. of Wyoming, Laramie, Ph.D. thesis. 144 pp.
Love, J. D., and J. C. Reed, Jr. 1968. Creation of the Teton Landscape: The Geologic Story of Grand Teton National Park. Grand Teton Natural History Association. 120 pp.
Orloci, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecology 54: 193-215.
Oswald, E. T. 1966. A Synecological Study of the Forested Moraines of the Valley Floor of Grand Teton National Park, Wyoming. Montana State University, Bozeman, Ph.D. thesis. 101 pp.
Reed, J. F. 1952. Vegetation of Jackson Hole Wildlife Park, Wyoming. Amer. Midl. Nat. 48: 700-729.
Sabinske, D. W. 1972. The Sagebrush Community of Grand Teton National Park: A Vegetation Analysis. Univ. of Wyoming, Laramie, M.S. thesis. 56 pp.
Shaw, R. J. 1976. Field Guide to the Vascular Plants of Grand Teton National Park and Teton County, Wyoming. Utah State Univ. Press, Logan, Utah. 301 pp.
Summerfield, H. B., and F. F. Peterson. 1971. Soil properties related to occurrence of big and low sagebrush in northwestern Nevada. Abstract of Papers, 24th Annual Meeting, Society for Range Management, Reno, Nevada.

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New Plant Records for Idaho from Pacific Coastal Refugia[1]

Abstract

Thirteen species of vascular plants unreported or unconfirmed for Idaho are discussed. Twelve of these taxa have their major distribution west of the Cascade Mountains. The Idaho populations are disjunct and are found in refugia where there are high numbers of other coastal disjuncts such as *Alnus rubra* and *Cornus nuttallii*. The ecology of these species is discussed.

Introduction

Recent studies of disjunct Pacific coastal forest communities in northern Idaho (Johnson, 1968; Roper, 1969; Steele, 1971; Graf, 1974) have yielded several new plant records and have clarified the reported existence of other taxa. It is ecologically significant that most of these plants occur very locally in the lower canyons of the Selway, Lochsa, and North Fork Clearwater Rivers. In these valleys, plant communities and climate exhibit a close resemblance to communities and climate west of the Cascade Mountains. Locations for many of these new records coincide with inland disjunct distribution of *Alnus rubra*[2] and to a lesser degree of *Cornus nuttallii*. These areas are refugia, and Steele (1970) discusses the occurrence of many of these species in disjunct forest associations; Graf (1974) develops a summary of knowledge of disjunct vegetation associated with *Alnus rubra* in the northern Rockies. Daubenmire (1975) provides a floristic history of northern Rockies and postulates how these disjunct and endemic populations in northern Idaho owe their existence to major refugia there.

The principal range descriptions herein are condensed from Hitchcock *et al.* (1955, 1959, 1961, 1964, 1969), with some modifications by Hitchcock and Cronquist (1973). Davis (1952), St. John (1963), and Taylor (1970) were also consulted. State abbreviations are those of the U.S. Postal Service. The following herbaria were searched for Idaho and northern Rocky Mountains collections; U. of Idaho (ID), U. of Idaho-Forestry (IDF), Washington State U. (WS), Idaho State U. (IDS), Boise State U. (BS), Oregon State U. (OSC), U. of Oregon (ORE), Intermountain Forest and Range

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[2]Scientific names follow Hitchcock and Cronquist, 1973; authors are omitted except for subject plants.

Exp. Sta., (USFS), Boise (BOIS), U. of Washington (WTU), and the U.S. National (US), and in some cases the Intermountain Forest and Range Exp. Sta. in Missoula, MT (MRC).

Voucher specimens are deposited in the Forest, Wildlife and Range Exp. Sta. Research Herbarium (IDF) of the University of Idaho; duplicates of most collections are in the University of Idaho Herbarium (ID), and selected duplicates were sent to other herbaria listed. Identifications are those of the authors and confirmations are noted. Forest associations and habitat types (h.t.) follow Daubenmire and Daubenmire (1968), or Steele (1970). Observations are based on five seasons of field work in most of the areas mentioned. Listing is phylogenetic. All collections are from Idaho; legal locations all refer to the Boise Meridian, Idaho.

The Plant Records

1. *Equisetum telmateia* Ehrh. (Equisetaceae). This giant horsetail was reported for Idaho by Davis (1952). Probably this report was based on a collection by W. H. Baker (6608-ID) taken 12.8 km w. of Orofino in Clearwater Co. Hitchcock *et al.* (1969), Hitchcock and Cronquist (1973), and Taylor (1970) however, report it as entirely west of the Cascades, where it ranges from s. AK to CA.

This species is common in moist streambottoms, particularly beneath *Alnus rubra*, (Steele, 7068; Johnson and Steele, 74279) along the N. Fk. Clearwater Riv. from the mouth of the Little North Fork to Aquarius Campground. Identification was confirmed by C. L. Hitchcock. The Dworshak Reservoir has recently inundated perhaps 75 percent of this population. It also occurs along small tributaries of the lower Lochsa (Steele, 70102), Selway, and Middle Fk. Clearwater Rivers, usually beneath *Alnus rubra* or *A. rubra* X *incana* hybrids. Baker's collection represents a small colony which occurs with *Alnus rubra* and *Thuja plicata* along the main Clearwater Riv. well below these main upstream populations.

2. *Dryopteris arguta* (Kaulf.) Watt. (Polypodiaceae). This fern occurs chiefly west of the Cascades from s. B.C. to s. CA and e. to AZ (disjunct); it has been reported from Stevens County, in n.e. WN. The range mapped by Taylor (1970) is entirely w. of the Cascades.

The first Idaho collection (Steele & Johnson, 70147) was made near the mouth of Beaver Cr., N. Fk. Clearwater Riv., (Sec. 6, T40N, R7E, elev. 510 m) in a mature *Thuja plicata/Dryopteris austriaca-D. filix-mas* association in a riparian habitat. A second collection (Johnson, 70176) was made from upper Minnesaka Cr., about 5 airkilometers north in a similar habitat. Identification of these specimens and other listed ferns was confirmed by David Wagner, University of Oregon.

This fern is apparently quite uncommon in the area where these specimens occurred, for despite further searching in apparently suitable habitats, no other individuals were found.

3. *Polypodium glycyrrhiza* D. C. Eat. (Polypodiaceae). Hitchcock *et al.* (1969) and Taylor (1970) describe this fern as a Pacific coastal species distributed from AK to CA, exclusively w. of the Cascade/Sierra Nevada crest except for a small intrusion into the Columbia River gorge. Lange (1969) discusses and maps northwestern species in the *Polypodium hesperium* complex; he also shows *P. glycyrrhiza* entirely w. of the Cascades. The single Idaho collection (Johnson, 7165B) was made on a small

tributary of June Cr. above the N. Fk. Clearwater Riv. (Sec. 14, T40N, R7E; elev. 1070 m) on mossy granitic boulders beneath a *Thuja plicata* forest. Apparent intergrades between *P. glycyrrhiza* and *P. hesperium* also occur in this area (Johnson, 7159, 73690; Ownbey & Ward, 3130-WS), and the area supports the largest known population of *P. hesperium* in the Northern Rockies.

4. *Thelypteris nevadensis* (Baker) Clute ex Morton (Polypodiaceae). This fern is distributed west of the Cascade/Sierra axis from Mt. Rainier, WN, to c. CA. No collections have been found east of these mountains. We collected it (Johnson and Steele, 7156) along the Elmer Cr. trail in the Patriarch Grove of large *Thuja plicata*; this trail is on a tributary of Isabella Cr., about 3 km from the N. Fk. Clearwater Riv. (Sec. 9, T41N, R7E; elev. 1000 m). Several small patches growing with *Equisetum sylvaticum* were found in the overflow seepage from a spring in a mature *Thuja plicata/Athyrium filix-femina* association.

This fern is easily mistaken for immature fronds of the ubiquitous *Athyrium filix-femina* and thus could be easily overlooked. Nonetheless, once aware of its identity, extensive searching in apparently suitable habitats in our study area has proven fruitless.

5. *Juncus effusus* var *pacificus* Fern. & Wieg. (Juncaceae). The principal population of this rush is from the west slopes of the Cascades to the Pacific "where often in coastal bogs or even in tidal mud flats" they are found (Hitchcock *et al.* 1969).

Davis (1952) is the only flora checked that reports this species for Idaho, apparently based on a single collection near Caldwell (Canyon Co.), an unusually dry macro-habitat (sagebrush/grass formation) for a plant otherwise restricted to a maritime climate. This collection is recorded in the IDS register, but the specimen could not be located. A presumed duplicate at WS (Davis, 4086, 15 Sept. 1941) from Curtis Park (T4N, R3W) is noted "first Idaho collection," and was confirmed by F. J. Herman. Curtis Park is an area of undeveloped Boise River floodplain; some wet areas exist through most summers. Since waterfowl from the Pacific have been sighted in the vicinity, (R. D. Bratz, pers. comm.), they could have introduced seed from this coastal rush.

New Idaho collections (Steele, 6900, 6950; Johnson & Steele, 73712) were made along Beaver Cr. about 2 km above its confluence with the N. Fk. Clearwater Riv. (Sec. 6, T40N, R7E; elev. 520 m). It is well established on a mud flat in a badly disturbed riparian *Thuja plicata* stand. The collection was confirmed by C. L. Hitchcock.

6. *Cynosurus echinatus* L. (Gramineae). This introduced European grass is reported along the Pacific coast in s.w. B.C. and from the Willamette Valley, OR, to CA.

It was collected by L. L. Hooker near Bimerick Cr., at the Lochsa River in 1971 (7165; Sec. 3, T33N, R8E; elev. 610 m), where it was growing in a disturbed *Thuja plicata/Adiantum pedatum* h.t. This area served as a packer's camp for many years; it received heavy grazing use, and hay was often scattered about to feed the pack stock. Examination four years after the initial collection showed an apparently stable population, but the site had been abandoned as a pack camp. Thus, unless *Cynosurus* spreads to new disturbed areas, succession will likely wipe out this population. Confirmed by C. L. Hitchcock.

7. *Boykinia major* Gray var. *intermedia* Piper (Saxifragaceae). This plant was reported for Idaho by Davis (1952) as *B. intermedia* (Piper) G. N. Jones. It has since

lost recognition as an Idaho plant as it is not listed either in Hitchcock *et al.* (1961) or Hitchcock and Cronquist (1973); they report it from the Olympic Peninsula to Tillamook Co., OR. Steele collected this variety in Idaho near the mouth of Rye Patch Cr. on the Lochsa Riv. (697029-Sec. 22, T33N, R7E; elev. 480 m, Idaho Co.) in a disturbed riparian habitat. This area supports riparian *Alnus rubra* and *Equisetum telmateia* and upland populations of *Cornus nuttallii* as well as other coastal disjuncts. Confirmed by C. L. Hitchcock.

8. *Prunus avium* L. (Rosaceae). This large European tree is the parent of our commercial sweet cherries. Hitchcock *et al.* (1961) and Hitchcock and Cronquist (1973) both include this species, commonly called mazzard or bird cherry, in their keys; but there is no mention of its range. Franklin & Dyrness (1973) summarize community structure of some populations in w. OR. Neither Davis (1952) nor St. John (1963) list *P. avium.* Little (1953) makes no mention of this species escaping in the entire western U.S. Johnson (1966) notes its escape, but no details are provided. We have made observations as follows: a) along the Salmon and Little Salmon Rivers, and middle Snake River, Idaho Co. (Johnson, 697202), it has commonly escaped along streambottoms dominated by *Alnus rhombifolia* and is infrequent in streams dominated by *Populus trichocarpa*; b) in the canyon of the central Clearwater Riv., especially between Orofino and Kooskia (Clearwater and Idaho Counties), it is widely naturalized in disturbed *Pseudotsuga menziesii/Physocarpus malvaceus* h.t. (Johnson & Steele, 73685), often accompanied by escaped *Prunus spinosa*; c) along the Greer Grade (Johnson, 6632) above the Clearwater Riv. (State Highway 11, Clearwater Co.), it grows on dry ridges where ponderosa pine is climax over a disturbed grass understory. Here it is generally the only tree other than ponderosa pine; *P. avium* trees 9 to 12 m tall are not uncommon, with high numbers of smaller size classes. The notable droughts of 1967 and 1973 have had no noticeable effect on *P. avium* in these habitats, which are the driest seen for this species in Idaho. Interestingly, these lower canyons have mean annual temperatures (*c.* 12°C) almost identical to those given by Franklin & Dyrness (1973-p. 111) for Willamette Valley populations of *P. avium.*

9. *Prunus persica* (L.) Batsch (Rosaceae). The common peach has occasionally escaped in northern Idaho; this fact is mentioned by Johnson (1966), but details have not been specifically recorded in the literature. None of the local floras list this species for Idaho or the Pacific Northwest; Little (1953) does not list it as an escape in the w. U.S. Most often it is found in roadside gravels along the lower canyons in w. and c. ID. The first trees found away from roads, homesteads, orchards, etc., were saplings growing in a seral shrub community with *Holodiscus discolor, Physocarpus malvaceus, Acer glabrum* and other medium and tall shrubs in either an *Abies grandis* or *Thuja plicata* climax (Johnson, 73640). The site is on Smith Cr., above Syringa, Idaho (Sec. 32, T33N, R6E; elev. 910 m). Geographically this area lies near the downstream limits of the distribution of *Alnus rubra* and *Cornus nuttallii* and the associated coastal forest communities (Roper, 1969).

10. *Cytisus scoparius* (L.) Link. (Leguminosae). Scotch broom has very commonly escaped west of the Cascades from B.C. to CA, but it is not reported for the northern Rockies in any of the local floras.

There are several collections from n. Idaho, but established populations have not been confirmed in the literature. J. H. Christ (1458-ID) collected it in 1932 in Kootenai

County near Hayden Lake, noting "escape from cultivation." R. F. Daubenmire noted a population in 1946 as "well established locally" (46315-WS-St. Joe River, "probably Benewah County"). P. F. Stickney (363-MRC) collected from the Lochsa population described below in 1960. Johnson (6523-IDF-1965) collected from an escaped plant in roadside gravel along US-95A in Benewah Co. Layser and Phillips (1972) reported its occurrence along the St. Joe River (Shoshone Co.—Layser—1441-WS): they noted "several large bushes were observed growing in the wild," but no suggestion was made of an expanding population; however, they implied that these were escapes.

Two other populations have been found. One extends perhaps 200 m along the roadside (U.S. 12) and into adjacent disturbed forest near Apgar Cr. (Sec. 11, T33N, R7E; elev. 490 m, Idaho Co.) on the Lochsa Riv. on the disturbed edge of a *Thuja plicata/Adiantum pedatum* h.t. not far from riparian *Alnus rubra* (Johnson, 74463). Low temperatures in December 1972 resulted in death of about 90 percent of the above-ground parts. The damage pattern suggests that only branches beneath snow survived. Root and crown sprouts appeared abundantly the following spring, as did seedlings. By 1974 the population was again vigorous, and in 1976 the slow spread to adjacent disturbed habitats was continuing.

Another population, closely associated geographically with *Alnus rubra* (Graf, 1974), appears near Hope, Idaho (Sec. 34, T57N, R1E; elev. 650 m; Bonner Co.) at the north end of Pend Oreille Lk. (Graf, 73629). The plants occur on very thin soils in a disturbed *Pseudotsuga menziesii/ Physocarpus malvaceus* h.t. associated with shrubs typical to this community. The Scotch broom plants, according to a local gardener, are progeny of plants raised from seed brought from the Pacific coast about 1942. They have been observed escaping for at least 12 years. Larger plants are 1-2 m (3-7 ft) tall and the population is vigorous with seedlings common and spreading both along the forest edge and in roadside gravels. Like the Apgar populations, these are reported to freeze to the ground in some years, but appear to sprout vigorously. The Apgar population is entirely deep yellow-flowered, but the Hope population has both deep yellow and yellow/red flowers.

From the Pend Oreille, St. Joe, and Lochsa foci, it seems reasonable to expect a gradual spread of *Cytisus scoparius* in northern Idaho but only within the *Alnus rubra* zone. There seems to be little reason to expect or fear the extensive invasion seen on Pacific coastal areas. In Idaho *Cytisus scoparius* seems marginally cold-hardy in areas peripheral to *Thuja/Tsuga* forests and apparently is not coldhardy in these forest areas except at their warmer limits. The warmer parts of the *Thuja/Tsuga* forest are marked by the presence of *Alnus rubra* or *A. rubra* X *incana* hybrids. Downstream migration into warmer areas from these populations appears to be limited by either drought and/ or excessive heat and very probably by winter cold without snow cover.

11. *Viola sempervirens* Greene (Violaceae). This evergreen violet is widely distributed w. of the Cascades from B.C. to CA. Davis (1952), Hitchcock *et al.* (1961), and Hitchcock and Cronquist (1973) do not report it for Idaho, but St. John (1963) does. His report was probably based on a single collection (Reek, 38202-WS) taken in 1925, 9.6 km n.w. of Hayden Lk., Kootenai Co. No other trans-Cascadian plant is known to have a disjunct population in this locality, although *Alnus rubra* X *incana* hybrids occur around Hayden Lk. Recent collections of this *Viola* (Steele, 7151; Steele & Johnson, 73731; Graf, 72140) verify an established population along the N. Fk.

Clearwater Riv. from Beaver Cr. to Marquette Cr. (T41N, R6E; elev. 500-550 m). It grows here beneath seral *Alnus rubra* and in mature *Thuja plicata/Adiantum pedatum* associations. It is reasonably common, once distinguished from the similar *V. orbiculata,* with which it often associates. Since its discovery, we have searched for this plant in other areas in the range of *Alnus rubra* and other coastal disjuncts, but have found none.

12. *Dodecatheon hendersonii* Gray (Primulaceae). This shooting star is found west of the Cascades from Vancouver Island to s. CA, but has not been reported from the n. Rockies. The only Idaho collection (Steele, 7037; Sec. 30, T32N, R9E; elev. 485 m; Idaho Co.) was made just above the Selway Riv. on Cache Cr. It grows here on the lower slopes of the canyon beneath a mature *Thuja plicata/Adiantum pedatum* association. Again, this plant is in an *Alnus rubra* zone and geographically associated with other coastal disjunct species. The specimen was confirmed by C. L. Hitchcock.

13. *Digitalis pupurea* L. (Scrophulariaceae). This Eurasian garden foxglove is well established w. of the Cascades and is "occasionally farther east" (Hitchcock & Cronquist, 1973). How much farther east seems an open question. Davis (1952) and St. John (1963) do not report it for Idaho. Hopefully, this omission is due to reluctance to add alien taxa until establishment is confirmed. For example, Pickett (105029-WS) made a collection on the Little N. Fk. Clearwater Riv. in 1917, noting: "common in homestead clearings." E. C. Trivette made a collection in 1951, 8 km s.e. of Potlatch (205744-WS), but this site would be in farming country, so establishment might easily be questioned.

We feel that this plant has escaped and is naturalized in Idaho. We have observed it in disturbed habitats on the lower St. Joe Riv. (Shoshone Co.); along the Little N. Fk. Clearwater Riv. (Steele, 7026; T41N, R5E; elev. c. 600 m); at Apgar Cr. on the Lochsa Riv. (See #1—*Equisetum telmateia*); on dredge-tailings along the upper Palouse Riv. (Latah Co.), where E. M. Hurley (59051-ID) collected specimens in 1962 with the notation "found for 50 yds. along the roadside"; and near Syringa, on the Middle Fk. Clearwater Riv. (Idaho Co.). Graf (73548; Sec. 27, T57N, R1W; Bonner Co.; elev. 700 m) collected from a population near Pend Oreille Lk. in a disturbed *Tsuga heterophylla/Pachistima myrsinites* h.t. which contained seral *Alnus rubra.* All of these areas contain concentrations of coastal disjuncts. The Little N. Fk., Apgar, Syringa, and Pend Oreille Lk. sites are in the *Alnus rubra* zone, already discussed. The Palouse Riv. and St. Joe Riv. areas are within populations of *Alnus rubra* X *incana* as well as other coastal disjuncts such as *Physocarpus capitatus, Symphoricarpos mollis,* and *Berberis nervosa.* All of these sites occur near the lowest elevations in which *Thuja plicata* is climax, and we believe that continued spread in such areas is likely.

Summary

Thirteen species are here confirmed as present in northern Idaho. Eight of these species (#1, 2, 3, 4, 5, 7, 11, & 12) are plants whose major populations are native west of the Cascade Mountains in adjacent Washington and Oregon, where they are all associated with the extensive maritime forest of *Thuja plicata, Tsuga heterophylla,* and *Alnus rubra.* In northern Idaho these species associate with the same major trees in refugia of coastal affinities.

Five of these species (#6, 8, 9, 10, & 13) are alien taxa from Eurasia; all of

these except #9 have escaped widely west of the Cascades. In northern Idaho, these species except #8 thus far appear confined to the general areas as native coastal disjuncts. All but two (#6 & 9) of these aliens have firmly established reproducing populations in northern Idaho.

Literature Cited

Daubenmire, R. F., and J. B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Wash. Ag. Exp. Sta. Tech. Bull. No. 60, Coll. of Agric., Wash. State Univ. 104 pp.

————. 1975. Floristic plant geography of eastern Washington and northern Idaho. Jour. Biogeog. 2: 1-18.

Davis, R. J. 1952. Flora of Idaho. Wm. C. Brown Co., Inc., Dubuque, Iowa. 828 pp.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. USDA-FA-Genl. Tech. Rept. PNW-8, Portland, Oregon. 417 pp.

Graf, P. E. 1974. Successional Stages of Red Alder in Bonner County, Idaho. Univ. of Idaho, Moscow, M.S. thesis. 146 pp.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. of Wash. Press. 730 pp.

————, ————, M. Ownbey, and J. W. Thompson. 1955, 1959, 1961, 1964, 1969. Vascular Plants of the Pacific Northwest. Parts 1-5. Univ. of Wash. Press.

Johnson, F. D. 1966. Native Trees of Idaho. Idaho Ag. Ext. Bull. 289. Univ. of Idaho. 36 pp.

————. 1968. Disjunct populations of red alder in Idaho, pp. 1-8. *In* Biology of Alder. J. M. Trappe, J. F. Franklin, R. F. Tarrant, and G. M. Hanson (ed.) Pac. Northwest For. & Range Expt. Sta., Portland. 292 pp.

Lang, F. A. 1969. A new name for a species of *Polypodium* from northwestern North America. Madroño 20: 4, April.

Layser, E., and H. W. Phillips. 1972. *Cytisus scoparius* (L.) Link in North Central Idaho, Madroño 21: 7, July.

Little, E. L., Jr. 1953. Checklist of Native and Naturalized Trees of the United States. USDA Ag. Handbook #41. Washington, D.C. 472 pp.

Miller, T. B. 1976. Ecology of Riparian Communities Dominated by White Alder in Western Idaho. Univ. of Idaho, Moscow, M.S. thesis. 154 pp.

Roper, L. A. 1970. Synecology of *Cornus nuttallii* in northern Idaho. Univ. of Idaho, Moscow, M.S. thesis. 81 pp.

St. John, H. 1963. Flora of Southeastern Washington and Adjacent Idaho. Outdoor Pictures, Escondido, California. 583 pp.

Steele, R. W. 1970. Red Alder Habitat in Clearwater County, Idaho. Univ. of Idaho, Moscow, M.S. thesis. 88 pp.

Taylor, T. M. C. 1970. Pacific Northwest Ferns and Their Allies. Univ. of Toronto Press. 247 pp.

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Relationship of Cover Type to Altitude, Aspect, and Substrate in the Bridger Range, Montana

Abstract

Point enumeration data taken from topographic, timber type, and geologic maps were used to relate cover type to elevation, aspect, and substrate in the Bridger Range, Montana. Douglas-fir forests are dominant. Grasses and shrubs attain high cover at low elevations (1678 to 1983 m) and on ESE and SSW slopes. Subalpine fir increases in importance at elevations over 2288 m. Lodgepole pine occurs at all elevations, but only on NNE and ESE aspects. Cover type is clearly related to substrate: Douglas-fir prefers limestone and gneiss; grasses prefer sandstone; lodgepole pine prefers interbedded sandstone and shale; and subalpine fir rarely occurs on gneiss. Possible ecological relationships and applications are discussed.

Introduction

The Bridger Range is a small, isolated mountain range in south central Montana. It extends from 110°53′ to 111°6′ west longitude, 45°40′ to 46°10′ north latitude, and from 1525 to 2948 m. Its topography, geology, and vegetation cover types have been mapped by U.S. Geological Survey (1949-1953), McMannis (1955), and U.S. Forest Service (1960-1962). Weather stations at Bozeman, Bangtail Ridge, and Bridger Ridge represent the area (U.S. Weather Bureau, 1971-1972; and Arlin Super, pers. comm.). The objects of this paper are 1) to summarize this information, and 2) to relate the cover types to altitude, aspect, and substrate.

Methods

Vegetational cover, altitude, slope, aspect, and substrate were measured at 555 regularly spaced points in the Bridger Range. 1) The range was delineated by a line following the 1678 m (5500 ft) contour on its north, west, and south sides and on the east side by Bridger and Bracket Creeks, which separate the Bridger Range from the Bangtail Range. 2) Four points were sampled in each section (square mile), including one at its NE corner, one midway between the NE and SE corners, one midway between the NE and NW corners, and one at the center of the section. 3) Altitude, aspect, and slope were recorded for each point from U.S. Geological Survey topographic maps. Altitude was recorded to the nearest 30 m (100 ft). Aspect was recorded in classes centered on N, NE, E, SE, S, SW, W, and NW; for much of the discussion these were pooled by twos into classes centered on NNE, ESE, SSW, and WNW. Slopes were recorded in the following classes: 0-8 percent, 8-16 percent, 16-32 percent, 32-64 percent, and 64-100 percent. 4) The cover at each point was categorized as bare ground, grass-shrubland, Douglas-fir forest, lodgepole pine forest, or subalpine fir forests. Timber

types were determined from U.S. Forest Service timber type maps. When points fell in areas of nonforest or noncommercial forest, aerial photographs were consulted to determine the cover type. Most of the vegetation considered is similar to Daubenmire's (1968, 1970) *Agropyron spicatum-Poa secunda, A. spictatum-Festuca idahoensis, Artemisia tridentata-F, idahoensis, Pseudotsuga menziesii-Symphoricarpos albus, P. menziesii-Calamagrostis rubescens, Abies lasiocarpa-Vaccinium scoparium*, and tundra associations. 5) Substrates were determined from McMannis' (1955) geologic map of the Bridger Range under his guidance; they included gneiss, limestone, sandstone, and interbedded sandstones and shales.

Climate of the Bridger Range

Mean (1970-1972) daily maximum temperature, mean daily minimum temperature, and mean precipitation are summarized by month in Figure 1 for stations at 1481, 2242, and 2590 m (4856, 7352, and 8500 ft). Precipitation and summer temperature data are unavailable for the 2590 m "Bridger Ridge" site. The short 1970-1972 record was used because no longer record exists for either the 2590 m or the 2242 m "Bangtail Ridge" site; the longterm weather record at Bozeman (MSU) shows the 1970-1972 period was near normal except that September precipitation was approximately 150 percent of normal, February temperatures were 4.4°C above normal, August temperatures were 2.8°C above normal, and October temperatures were 3.3°C below normal.

In the grassy (*Festuca idahoensis-Agropyron spicatum*) foothills zone (Bozeman, 1481 m), temperatures in January ranged from –10° to 0°C (mean daily minimum and mean daily maximum), July temperatures were in the 11° to 28°C range, and the moist spring (5 cm/month) was followed by a dry summer and winter (1.9 cm/month). High in the Douglas-fir zone (Bangtail Ridge, 2242 m), January temperatures

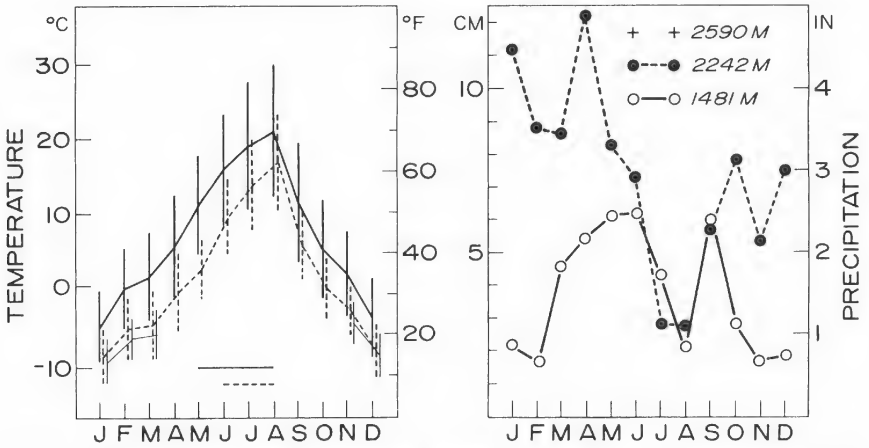

Figure 1. Climatic data at three Bridger Range weather stations: Bozeman (1481 m, heavy solid line), Bangtail Ridge (2242 m, broken line), and Bridger Ridge (2590 m, light solid line). In the temperature graph, lines show average temperatures and vertical bars indicate average daily maxima and minima for each month. Horizontal lines indicate months with less than 3 frost days. Data for precipitation and summer temperature are unavailable for Bridger Ridge.

were in the –12° to –6°C range, July temperatures were in the 8° to 20°C range, and except for the dry summer (3 cm/month), rainfall generally exceeded 5.7 cm per month. January temperatures high in the subalpine-fir zone (Bridger Ridge, 2590 m) were also in the –12° to –6°C range. Climates of a nearby Idaho-fescue grassland (2166 m) and a nearby whitebark pine stand (2257 m) are discussed by Mueggler (1971) and Weaver and Dale (1974), respectively: temperatures are similar to those reported here; precipitation patterns include the May-June high and the July-August low seen in the Bridgers, but precipitation in the whitebark pine stand is significantly greater than in the other local vegetation types.

0.55° to 0.73°C per 100 m is a commonly cited average lapse rate (e.g., Oosting, 1956; Bamberg and Major, 1968). In the Bridgers, average temperature dropped 0.89°C with a 100 m increase in altitude agreeing with Peattie's (1936) observation that small mountain ranges are cooler at a given altitude than larger ones. The lapse rate was steeper at the daily maximum temperature (1.0°/100 m) than at the daily minimum temperature (0.42°/100 m).

Effective precipitation may be greater on the east than on the west side of the Bridger range: total precipitation is likely to be similar on both sides, but 1) temperatures and evaporation rates are usually higher on west than on east slopes (Geiger, 1965); and 2) the western side is bordered by the broad Gallatin Valley and the eastern side is sheltered by a narrow valley and the Bangtail Ridge.

Relationship of Slope, Aspect, Substrate, and Cover to Altitude

Three altitudinal zones are used in the descriptions and analyses presented below: low (1678-1982 m = 5500-6500 ft), middle (1982-2288 m = 6500-7500 ft), and high (2288-2593 m = 7500-8500 ft). These comprised 41, 39, and 19 percent of the study area respectively; the 2 percent which lay above 2593 m was pooled with the 2288-2593 m stratum. Median slopes in these zones were approximately 24, 48, and 64 percent, respectively. Aspects were evenly divided at 1678-1982 m: 26 NNE, 28 ESE, 24 SSW, and 23 percent WNW. Corresponding figures at 1982-2288 m and 2288-2593 m were 28, 29, 22, and 21 percent; and 24, 28, 30, and 18 percent. Sandstone, sandstone-shale, gneiss, and limestone covered 25, 35, 30, and 10 percent of the low zone; 11 49, 20, and 20 percent of the middle zone; and 9, 15, 44, and 32 percent of the high zone, respectively.

The amount of bare ground increased strikingly with altitude; we measured 1, 1, 10, and 69 percent at 1678-1982, 1982-2288, 2288-2593, and above 2593 m, respectively. Of the 22 bare ground sites above 2288 m, two were on sandstone, two were on sandstone-shale, and 18 were on limestone. Half of those faced ESE, 25 percent faced SSW, 17 percent faced NNE, and 8 percent faced WNW. One bare WNW-facing sandstone site and one bare ESE-facing sandstone-shale site lay below 2288 m. Bare sites were included in the calculations of percentages of the area covered by various vegetation types presented below.

The dominant cover of the Bridger Range is Douglas-fir; at lower altitudes grasslands increase in importance and at higher altitudes subalpine-fir increased in importance (Fig. 2). Essentially all the area below 1678 m is grassland. The vegetation of the 1678-1982 m zone is 38 percent grass, 47 percent Douglas-fir, 15 percent lodgepole pine, and 0 percent subalpine fir. In the 1982-2288 m and 2288-2593 m

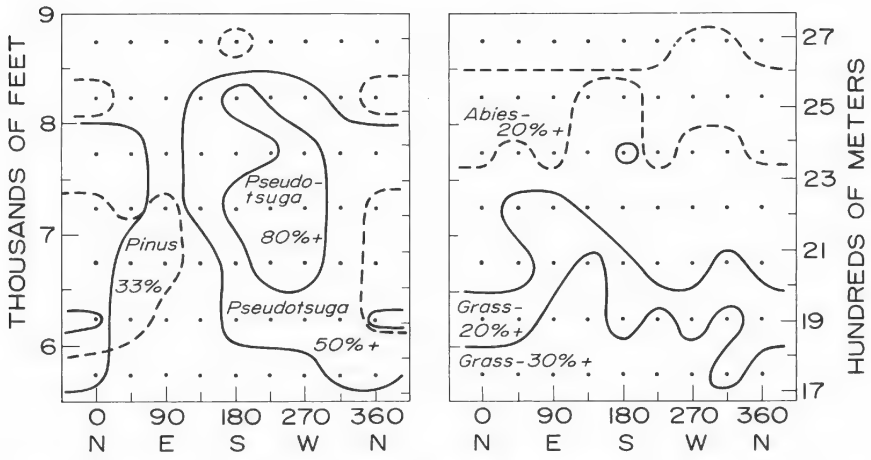

Figure 2. Distribution of grassland, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*) according to altitude and aspect in the Bridger Range. Isolines enclose areas in which each cover type is important: elevation-aspect conditions where *Pseudotsuga* covers more than 80 percent (50 percent) of the points sampled, *Pinus* coverage exceeds 33 percent, *Abies* coverage exceeds 20 percent, and grass coverage exceeds 30 percent (20 percent).

zones, the corresponding figures are 16, 61, 21, and 2 percent; and 10, 55, 12, and 19 percent. Three of the four vegetated sites above 2593 m were occupied by subalpine fir; the fourth was a lodgepole site.

Relationship of Vegetational Cover to Aspect

Vegetational cover is clearly related to aspect (Table 1 and Fig. 1). The grass-shrub type reaches its greatest cover values on southeast slopes (ESE and SSW); Douglas-fir is most important on southwest slopes (SSW and WNW); lodgepole is most important on northeast slopes (NNE and ESE); and until the 2288-2593 m level is reached subalpine fir also tends to occupy northeast slopes (NNE and ESE).

The behavior of the grasses and subalpine fir with changes in aspect mirrors their behavior with respect to altitude: grasses tend to dominate on warm dry sites and subalpine fir tends to dominate on cool moist sites.

At the 1678-1982 m and 1982-2288 m levels lodgepole pine is expected to be subclimax to Douglas-fir (e.g., Whitford and Craig, 1918), and might, therefore, be expected to occupy precisely the same sites Douglas-fir does. The observed segregation of the trees with respect to aspect mirrors relative water availability and suggests three hypotheses: 1) lodgepole pine may be climax on cool moist northeast facing slopes; 2) lodgepole is seral to Douglas-fir on northeast slopes, but not on southwest slopes which are usually too hot and/or dry for its establishment; or 3) lodgepole is seral to Douglas-fir, and probability of finding an early successional stage on a northeast facing slope is considerably greater than finding one on a southwest slope because it is in the northeast that stands are dense enough to carry crown fires regularly. The first hypothesis can be tested by looking for Douglas-fir reproduction in the northeast facing lodgepole stands; in Colorado Moir (1969) defined a logepole pine climax

zone, but felt that it was the result of high temperatures and drought rather than the opposite. The second hyothesis would be supported by Bates (1917), who reported that lodgepole has higher water requirements than either Douglas-fir or Englemann-spruce, and by Gail and Long (1935), who found it occupying hollows, gulches, and northeast-facing slopes. It would be questioned by Larsen (1930), Stephens (1966), and Despain (1973), who found lodgepole occupying relatively droughty sites. The second and third hypotheses are weakly supported by the near absence of lodgepole (6 percent) in the dry sites between 1678 and 1982 m.

TABLE 1. Cover type probabilities (percent) by elevation and aspect; figures give the percentage of elevation-aspect sites occupied by each cover type.

	Altitude (m[1])	NNE	ESE	SSW	WNW
Grass	1678-1982	33	45	40	30
	1982-2288	10	23	11	17
	2288-2593	8	3	15	10
	2593+	0	0	0	0
Douglas fir	1678-1982	39	35	56	62
	1982-2288	49	44	82	76
	2288-2593	38	35	58	75
	2593+	0	0	0	0
Lodgepole pine	1678-1982	28	18	4	6
	1982-2288	39	26	7	7
	2288-2593	19	16	3	5
	2593+	0	0	25	0
Subalpine fir	1678-1982	0	2	0	0
	1982-2288	2	5	0	0
	2288-2593	23	16	18	10
	2593+	0	0	0	60
Bare ground	1678-1982	0	0	0	2
	1982-2288	0	2	0	0
	2288-2593	12	29	9	0
	2593+	100	100	75	40

[1]In English units the altitudinal zones are: 5500-6500; 6500-7500; 7500-8500, and greater than 8500 ft.

Relationship of Vegetational Cover to Substrate

Vegetational cover is as clearly related to substrate as to aspect (Table 2). Limestone sites below 2440 m are dominated by Douglas-fir: Douglas-fir (67 percent) and grasses (25 percent) cover the low sites; Douglas-fir (95 percent) covers the middle altitude sites; and high sites are covered by Douglas-fir (40 percent), subalpine fir (21 percent), and grass (17 percent). Gneiss sites are dominated almost as strongly by Douglas-fir: Douglas-fir (61 percent) and grasses (32 percent) cover low sites; Douglas-fir (80 percent), lodgepole-pine (12 percent), and grass (5 percent) cover middle sites; and high sites are dominated by Douglas- fir (79 percent) and lodgepole pine (14 percent)—not subalpine-fir (3 percent). On sandstone sites grasses are especially important: low sites are 54 percent grass and 33 percent Douglas-fir; middle sites are 50 percent grass and 50 percent Douglas-fir; and high sites are 10 percent grass, 40 percent Douglas-fir, and 20 percent subalpine fir. On interbedded sandstone-shale substrates, lodgepole achieves its greatest importance, though Douglas-fir is still dominant: lodgepole (26 percent), Douglas-fir (39 percent), and grasses (35 percent)

cover low sites; lodgepole (37 percent), Douglas-fir (42 percent), and grasses (17 percent) cover middle altitude sites; and lodgepole (24 percent), Douglas-fir (41 percent), and subalpine fir (18 percent) cover high sites.

TABLE 2. Cover types by altitude and substrate; figures give the percentage of substrate-altitude sites occupied by each cover type.

	Altitude (m[1])	All Substrates	Sandstone	Sandstone-Shale	Gneiss	Limestone
Grass	1678-1830	52	60	67	48	30
	1830-1982	32	52	29	18	21
	1982-2135	19	47	21	11	5
	2135-2288	12	60	17	0	4
	2288-2440	5	0	0	8	14
	2440-2593	15	20	100	0	20
	2593+	0	0	0	0	0
Douglas-fir	1678-1830	42	33	25	48	60
	1830-1982	50	33	41	73	71
	1982-2135	55	53	38	79	95
	2135-2288	68	40	47	86	96
	2288-2440	63	40	44	85	71
	2440-2593	31	40	0	75	4
	2593+	0	0	0	0	0
Lodgepole pine	1678-1830	6	7	8	4	10
	1830-1982	18	10	29	9	7
	1982-2135	25	0	43	11	0
	2135-2288	16	0	28	14	0
	2288-2440	10	20	25	0	0
	2440-2593	13	0	0	25	4
	2593+	8	0	0	50	0
Subalpine fir	1678-1830	0	0	0	0	0
	1830-1982	1	2	0	0	0
	1982-2135	1	0	2	0	0
	2135-2288	3	0	7	0	0
	2288-2440	16	20	19	8	11
	2440-2593	19	20	0	0	32
	2593+	25	0	0	50	17

[1]In English units the altitudinal zones are: 5500-6000, 6000-6500, 6500-7000, 7000-7500, 7500-8000, 8000-8500, and 8500+ ft.

One might ask why lodgepole performs especially well on sandstone-shale; why grasses perform especially well on sandstone and so poorly on limestone; why subalpine fir performs poorly on gneiss; and why Douglas-fir performs better on limestone and gneiss than on sandstones and sandstone-shales. We can speculate as follows:

The importance of lodgepole on sandstone-shales might be due to fire or the high water and/or nutrient availability on sites with clay-rich soils, gentle slopes due to rapid weathering and/or slumping of shales, and/or high water tables. Several studies (Vlamis *et al.*, 1959; Williams *et al.*, 1963; Hough, 1943) have shown soils derived from shales and sandstone-shales to be more productive than sandstone, limestone, and granite soils. We doubt that lodgepole requires the relatively high nutrient availabilities associated with these soils because it seems to grow well on poor soils (Whitford and Craig, 1918; Stephens, 1916; and Despain, 1973). Gail and Long (1935) associate the presence of lodgepole pine with false hardpans and a high water table; their suggestion that lodgepole is most common on moist sites is consistent with the fact

that it is also most common on north- and east-facing slopes. The importance of lodgepole-pine on sandstone-shale substrates might not be directly due to requirements of the tree for either water or nutrients, but due instead to the high probability of fires in dense stands occuping these relatively rich sites.

Grass types may do well on sandstones because sandstones form well-drained soils which are too dry for competing cover types. Limestones are also expected to form well-drained soils, but here water storage in the upper horizons is probably reduced by stoniness; stoniness generally favors deep-rooted trees over shallow-rooted grasses (Walter, 1970; Despain, 1973). A lack of phosphorus on limestone sites may also favor Douglas-fir over the grasses (Gessel and Walker, 1958; Wright and Mooney, 1965).

The near absence of subalpine fir on the quartz-feldspar gneisses might be due to a high requirement for base-rich substrates or water. The high requirement for bases is suggested by its calcium-rich needles (Stottlemyer and Ralston, 1968) and by its inability to compete with whitebark pine on lime-poor soils at high altitudes (Weaver and Dale, 1974). The fact that the gneisses occur exclusively on the west side of the Bridgers suggests that gneiss sites might also be relatively dry.

Because Douglas-fir is the dominant tree of the Bridgers one may think of it as occupying those sites not especially favorable for other cover types: it apparently tends to be excluded from sandstones by competition with grasses and from sandstone-shales by lodgepole competition or fire.

Statistical Tests

We used Chi-square tests (5 percent level) to determine the significance of the observed changes. 1) The changes in species dominance with altitude and substrate are significant. The changes in species dominance with aspect are significant below 2288 m, but not significant above 2288 m. 2) Cover types did not change aspect significantly with changes in elevation. 3) Chi-square tests suggest that species do change substrates with elevation, but much of this effect appears to be due to the disappearance of sandstone and sandstone-shales at high elevation. 4) Chi-square analyses also suggest that Douglas-fir in the 1678-1982 and 1982-2288 m zones and grasses in the 1678-1982 m zone change aspect with substrate. At 1678-1982 m Douglas-fir is most frequent on WNW aspects of sandstone and sandstone-shale, while at 1982-2288 m it moves into the SSW ("drier" aspect) on sandstone-shale and the ESE ("wetter" aspect) on sandstones; it appears with equal (high) frequencies at both altitudes on limestone and gneiss. At 1678-1982 m grasses appeared with highest frequencies in the SSW on gneiss, sandstone-shales, and sandstones and in the NWN on limestones. In no altitudinal band did lodgepole pine change aspect with changes in substrate. The amount of subalpine fir was insignificant in the lower altitudinal zones.

Application

The strong relationships of vegetation cover to elevation, aspect, and substrate—whatever the causes may be—should be considered in management of mountain timberland. First, it may be difficult to regenerate a vegetation type after logging if it occupies a site unusual (marginal?) for it. It might be difficult, for example, to reestablish Douglas-fir on a low sandstone site. Second, when plantings are made, one

should select seedling stock known to thrive under available conditions: this study suggests that, in the Bridger Range, Douglas-fir has broad tolerance (i.e., can be planted almost anywhere) while lodgepole pine has narrower tolerances (i.e., will perform best on sandstone-shales and east-facing slopes).

Literature Cited

Bamberg, S., and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecol. Mono. 38: 127-167.

Bates, C. 1917. Biology of lodgepole pine as revealed by the behavior of its seed. J. Forestry 15: 410-416.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Wash. Ag. Expt. Sta. Tech. Bull. 62, Pullman. 131 pp.

————, and J. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Wash. Ag. Expt. Sta. Tech. Bull. 60, Pullman. 104 pp.

Despain, D. 1973. Vegetation of the Big Horn Mountains, Wyoming, in relation to substrate and climate. Ecol. Mono. 43: 329-355.

————. 1973. Major Vegetation Zones of Yellowstone National Park. USDI, National Park Service, Yellowstone National Park Information Paper 19. 4 pp.

Gail, F., and E. Long. 1935. A study of site, root development, and transpiration in relation to the distribution of *Pinus contorta.* Ecol. 16: 88-100.

Gessel, S., and R. Walker. 1958. Forest fertilization, pp. 20-30. Amer. Potash. Inst. Handbook. Washington, D.C. 57 pp.

Geiger, R. 1965. The Climate near the Ground. Harvard Univ. Press, Cambridge, Mass. 611 pp.

Hough, A. 1943. Soil factors and stand history in a virgin forest valley on the northern Allegheny Plateau. Soil Sci. 56: 19-28.

Larsen, J. 1930. Forest types of the northern Rocky Mountains and their climatic controls. Ecol. 11: 631-672.

McMannis, W. 1955. Geology of the Bridger Range, Montana. Bull. Geol. Soc. Amer. 68. 1385-1430.

Moir, W. 1969. The lodgepole pine (*Pinus contorta*) zone in Colorado. Amer. Midl. Nat. 81: 87-97.

Mueggler, W. 1971. Weather Variations on a Mountain Grassland in Southwestern Montana. U.S. Forest Service Reseach Paper Int-99. 25 pp.

Oosting, H. 1956. The Study of Plant Communities. Freeman, San Francisco. 440 pp.

Peattie, R. 1936. Mountain Geography: A Critique and Field Study. Harvard Univ. Press, Cambridge, Mass. 257 pp.

Stephens, F. 1966. Lodgepole pine-soil relations in the Oregon Cascade Mountains. J. Forestry 64: 184-186.

Stottlemyer, F., and C. Ralston. 1968. Nutrient balance relationships for watersheds of the Fraser experimental forest. *In* C. Youngberg and C. Davey (1968). Tree Growth and Forest Soils. Proceedings of the Third Amer. Soil Conf., Oregon State University Press, Corvallis, Oregon. 527 pp.

USDA Forest Service. 1960-1962. Gallatin National Forest Timber Inventory. Office of the Northern Region, Missoula, Montana.

U.S. Geological Survey. 1949-1953. Bozeman, Bozeman Pass, Sedan, Belgrade, Maudlow, and Hatfield Mountain Quadrangles. U.S. Geol. Survey, Washington, D.C. 6 pp.

U.S. Weather Bureau. 1971-1972. Climatological data: Montana section. U.S. Dept. of Commerce NOAA, Washington, D.C.

Vlamis, J., A. Schultz, and H. Biswell. 1959. Nutrient response of ponderosa pine and brush seedlings on forest and brush soils of California. Hilgardia 28: 239-254.

Walter, H. 1970. Vegetationszonen und Klima. Gustav Fischer Verlag, Jena. 244 pp.

Weaver, T., and D. Dale. 1974. *Pinus albicaulis* in central Montana: environment, vegetation, and production. Amer. Midl. Nat. 92: 222-230.

Whitford, H., and R. Craig. 1918. Forests of British Columbia. Committee on forests. Commission of Conservation, Ottawa. 69 pp.

Williams, J., A. Leven, and H. Dregne. 1968. Relation of soil properties to ponderosa pine production in the Zuni Mountains, New Mexico. *In* C. Youngberg and C. Davey (1968). Tree Growth and Forest Soils. Proceedings of the Third Amer. Soil Conf., Oregon State University Press, Corvallis, Oregon. 527 pp.

Wright, R., and H. Mooney. 1965. Substrate oriented distribution of bristle cone pine in the White Mountains of California. Amer. Midl. Nat. 73: 257-284.

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Contributions to the Flora of Washington. III

Abstract

Several new plant species and range extensions for the State of Washington are presented. Representative plants were collected by the authors in the foothills and mountains of Washington's North Cascades.

This article reflects the continued floristic studies in the Washington Cascades by the authors, especially Dorothy and Ralph Naas, who have spent several years in collecting plants and recording distributional data in connection with the North Cascades National Park and United States Forest Service. Based on the field work, herbarium studies, and literature review by the authors, a check list of North Cascades plants has been compiled. This check list and various floristic and ecological publications by the authors (Douglas, 1971, 1973; Douglas and Bliss, 1977; Douglas, Naas, and Naas, 1973; Douglas and Taylor, 1970; Taylor and Douglas, 1977; Taylor, Douglas, and Sundquist, 1973) should provide valuable assistance in a planned and much needed inventory of rare, threatened, and endangered species in the State of Washington.

Some of the plants treated herein are new records for Washington but most are range extensions, especially of plains and foothills species northward along the eastern Cascades into the Okanogan country. Such extensions were predictive with more complete floristic studies. Previously cited ranges for included taxa are taken from Hitchcock *et al.* (1955-1969) unless stated otherwise.

Specimens cited herein are presently located in one or more of the following herbaria: G. W. and G. G. Douglas (private), Victoria, B.C. (GD); United States Forest Service Herbarium, Fort Collins, Colorado (FS); North Cascades National Park, Sedro Woolley, Washington (NC); New York Botanical Garden Herbarium, New York, N.Y. (NY); Skagit Valley College Herbarium, Mount Vernon, Washington (SV);

University of Washington Herbarium, Seattle, Washington (UW); Western Washington University Herbarium, Bellingham, Washington (WW); and United States Forest Service, Winthrop, Washington (WI). Nomenclatural determinations were made by the authors unless otherwise noted.

New Plant Species and Range Extensions

Agastache urticifolia (Benth.) Kuntze var. *urticifolia.* Ten km southeast of Winthrop, Okanogan County, at elevation ca 870 m, *Naas & Naas 2790* (SV, WW). The plant was abundant on moist ground adjacent to a lake shore in a community of *Symphoricarpos albus, Rosa* species, and forbs. In Washington, this plant had not previously been reported to occur west of Grand Coulee Dam.

Carex atrata L. var. *erecta* W. Boott (*C. epapillosa* Mackenzie; *C. heteroneura* W. Boott). Hart's Pass, one km northeast of the ranger station, Whatcom County, elevation ca 2010 m; *Naas & Naas 1926* (FS, NC). This collection was made on the west aspect of an open, gravelly slope. Previously, this taxon had been reported only as far north as Mt. Adams, Washington. Its typical range includes the Sierra Nevadas and Southern Cascades. The identification to species and variety was made by F. J. Hermann.

Carex comosa Boott (*C. pseudo-cyperus* var. *comosa* Boott). Grandy Lake, 5.5 km northwest of Concrete, Skagit County, elevation ca 245 m; *Naas & Cheney 2091* (FS, NC). This plant was found growing in boggy soil along the lake shore. *Carex comosa* is an eastern North American species with rare, disjunct populations occurring in the Pacific States, from Washington and northern Idaho to California. Identification was made by F. J. Hermann.

Carex jonesii L. H. Bailey (*C. nervina* var. *jonesii* Kuekenth.). Hart's Pass, one km northeast of the ranger station, Whatcom County, elevation ca 1980 m; *Naas & Naas 1925* (FS, NC). This species was found in an open, boggy meadow, growing in association with *Eriophorum polystachion* and other *Carex* species. Previously it was known to range in the Pacific States from southern California to Mt. Adams, Washington. Identification was made by F. J. Hermann.

Carex paupercula Michx. Roger Lake, 25 km northeast of Winthrop, Okanogan County, elevation ca 1800 m; *Naas & Naas 2620* (FS, WI). This sedge was growing in seepage channels of boggy ground surrounding Roger Lake. It is a circumboreal species extending southward at increasing elevations to Colorado. This collection may be the first of this taxon in Washington. Identification was made by F. J. Hermann.

Carex stenophylla Wahl. (*C. eleocharis* L. H. Bailey; *C. stenophylla* spp. *eleocharis* Hulten; *C. stenophylla* var. *eleocharis* Breit.; *Vignea Stenophylla* Reichb.). Conconully, Okanogan County, elevation ca 705 m; *Naas & Naas 2105* (FS, WI). This plant was growing along a dry, gravelly roadside in association with *Centauria diffusa.* Previously it was known from the northern Great Plains to the east base of the Rocky Mountains, and at scattered locations in S.E. British Columbia, Idaho, Oregon, Nevada, and Arizona. This collection is apparently the first record from Washington. The identification was made by F. J. Hermann.

Collomia tenella Gray (*Gilia leptotes* Gray; *G. tenella* Nels. & Macbr.; *Navarretia leptotes* Kuntze). Thirty-five km north-northwest of Winthrop, Okanogan County, elevation ca 1325 m; *Naas & Naas 2361* (WI). This collection, taken from an open, vernally damp, rocky site, represents a northern range extension. Previously this taxon

was known from central Washington to northwest Wyoming, southward to Utah and Nevada.

Heuchera cylindrica Dougl. ex Hook. var. *alpina* Wats (*H. cylindrica* var. *ovalifolia* Wheelock; *H. ovalifolia* var. *alpina* Rosend.). Three km north of Conconully, Okanogan County, elevation ca 1100 m; *Naas & Naas 2122* (WI). This plant was common on the southwesterly aspect of a steep rocky ridge. Although this taxon is common in the Pacific States, it had not been previously reported north of the Wenatchee Mountains in Chelan County, Washington.

Humulus lupulus L. One km southeast of Rockport, Skagit County, elevation ca 70 m; *Naas & Cheney 1333* (NC, SV). This introduced vine was present over a wide area, clambering over such common shrubs as *Rubus spectabilis, Symphoricarpos albus,* and *Rosa* species. Although this species has often been observed growing outside of cultivation, according to Hitchcock *et al.* (1964), it was previously thought not to be established in the Pacific Northwest "except possibly in Montana."

Hypericum majus (Gray) Britt. (*H. canadense* var. *majus* Gray). Five km northwest of Concrete, Skagit County, elevation ca 245 m; *Naas & Cheney 2088* (NC, SV), *Naas & Cheney 2751* (UW, WW). The plants of collection 2088 were growing in boggy soil with *Mentha arvensis*. Plants of collection 2751 were growing in 2 cm of water in association with *Typha latifolia, Potentilla palustris,* and *Carex* and *Juncus* species. The latter habitat was probably unusually wet for *Hypericum* but had only recently been flooded by beaver dam construction. This taxon was collected in 1891 at Green Lake, Seattle, but prior to the Naas & Cheney collections was otherwise not reported from Washington. The range of the species includes Canada, British Columbia to Quebec, and southward in the central and eastern U.S.

The characteristics of this species are not well defined, overlapping with those of *H. anagalloides*. Possibly a more realistic treatment of the two taxa would be to consider them as geographical variants of the same species. Identification of collection 2751 was confirmed by Melinda Denton.

Juncus supinus Moench. (*Phylloschoenus supinus* Fourr.). Five km north-northeast of Sultan, Snohomish County, elevation ca 215 m; *Naas & Naas 1992* (FS, NC). This rush was growing on a floating log in a muddy-bottomed lake. This is a European species which was previously known in the Pacific Northwest from a single location, near Duval, Snohomish County. The identification was made by Charles Feddema.

Lupinus lepidus Dougl. ex Lindl. var. *aridus* (Dougl.) Jeps. (*L. aridus* Dougl. ex Lindl.; *L. hellerae* Heller; *L. piperi* Robins. ex Piper; *L. minutifolius* Eastw.; *L. lenorensis* C. P. Smith; *L. longivallis* C. P. Smith; *L. lepidus* ssp. *medius* Detling). Fourteen km northeast of Mazama, Okanogan County, elevation ca 1860 m; *Naas & Cheney 1621* (NC). This collection was taken from a population growing on flat scree on a dry, exposed, rocky butte. This taxon was previously not known to extend northward beyond central Washington from where it extends south to northern California and Nevada and east to central Idaho.

Lythrum salicaria L. One and a half km northeast of Okanogan, Okanogan County, elevation ca 260 m; *Naas & Naas 2565* (UW, WW). This introduced species, a native of Europe, was abundant in an open swampy area in association with *Typha latifolia.* Previously it had been reported only from the Puget Sound area. The identification was confirmed by Melinda Denton.

Madia sativa Mol. var. *sativa* (*M. capitata* Nutt.). Seven km southeast of Mazama,

Okanogan County, elevation ca 610 m; *Naas & Naas 2627* (FS, WI). This taxon was scattered along an open moist streambank in association with *Conyza canadensis* and various grasses. Previously it had been reported only from the west side of the Cascades, from northern Washington to California. Identification was confirmed by Charles Feddema.

Mimulus pulsiferae Gray. Seven km southeast of Mazama, Okanogan County, elevation 610 m; *Naas & Naas 2626* (WI, WW). This collection was taken from a population growing in an open, damp, mixed mud and gravel streambed. This rare plant is seldom collected and was not previously reported north of Klickitat County in Washington, whence it ranges southward.

Mimulus suksdorfii Gray. Hoodoo Pass, 50 km northwest of Chelan, Chelan County, elevation ca 2165 m; *Naas & Naas 998* (WW). This tiny monkey flower was abundant on a steep scree and talus slope, on a south aspect, in an open *Juniperus communis* community. Previously, the species was not known to occur north of Mt. Adams, from where it extends southward east of the Cascade Crest into California, and eastward to Wyoming and Colorado.

Nemophila parviflora Dougl. var. *austiniae* (Eastw.) Brand (*N. austiniae* Eastw.; *Viticella parviflora* var. *austiniae* Macbr.). Six km southwest of Marblemount, Skagit County, elevation ca 91 m; *Naas & Naas 3388* (NC, WW). This rare annual was collected on the edge of a lightly used gravel road, shaded by *Acer macrophyllum* and *Corylus cornuta.* It had not previously been known to occur west of the Cascade Crest, ranging from British Columbia on the east side of the Cascades to California and eastward to Utah.

Papaver argemone L. Oak Harbor, Island County, elevation ca 10 m; *Naas & Naas* (no number) (SV). This collection was taken from a gravelly roadside and was observed in fields and other disturbed areas. Previously, this introduction from Europe had been reported in Washington only on the east side of the Cascades.

Phacelia humilis T.&G. (*P. violacea* Brand). Thirty-five km north-northwest of Winthrop, Okanogan County, elevation ca 1325 m; *Naas & Naas,* 2353 (WI). This small annual was common along a roadside dominated by such weedy species as *Taraxacum officinale* and *Thlaspi arvense.* The previous known range was central Washington, southward along the east slopes of the Cascades and Sierras and adjacent plains.

Pohlia erecta Lindl. Chowder Ridge, above Cougar Divide, Whatcom County, elevation ca 2123 m; *Basabe 42* (WW). This small moss was found growing in pockets of soil on a scree slope, south aspect. It was associated with *Sedum lanceolatum, Phlox diffusa,* and *Silene acaulis.* Previously, it had been reported from only two locations in western North America, one collection from Mt. Rainier, Washington, and one collection from British Columbia. The identification was confirmed by W. B. Schofield.

Polygonum majus (Meisn.) Piper (*P. coarctatum* var. *majus* Meisn. in DC.). Twenty-six km east-southeast of Marblemount, Skagit County, elevation ca 846 m; *Naas & Naas 3433* (WW). This annual was an occasional plant on open, gravelly, disturbed soil at this location. The previous range was known to be the east base of the North Cascades, south to California, and east to Idaho and Montana.

Potentilla recta L. (*Hypargyrium rectum* Fourr.). Three km north of Marblemount, Skagit County, elevation ca 105 m; *Naas & Naas 563* (NC, WW). This European introduction was collected in an open, grassy field. It had been previously reported in

the Pacific Northwest from eastern Washington and northwestern Montana.

Sambucus racemosa L. var. *melanocarpa* (Gray) McMinn (*S. melanocarpa* Gray). Eight-mile Creek Valley, 31.5 km north-northwest of Winthrop, Okanogan County, elevation ca 1160 m; *Naas & Naas 2711, 2848* (WI, UW, WW). This shrub was abundant at this location and was collected on an open, rocky slope, northerly aspect, in association with *Rubus idaeus* and *Epilobium angustifolium.* It was also observed in the Loup Loup area of Okanogan County and has been reported elsewhere without documentation. The range of this taxon is primarily in the Rocky Mountains and had previously been known to occur in southern Washington, extending to the Mt. Adams area. Identification was confirmed by Melinda Denton.

Sanicula marilandica L. (*S. canadensis* var. *marilandica* Hitchc.; *Caucalis marilandica* Crantz.). Twenty-one km north of Winthrop, Okanogan County, elevation ca 670 m; *Naas & Naas 2306* (WI, WW). This species was an occasional inhabitant in an open spruce (*Picea engelmannii*) forest, growing on damp, silty soil. *Alnus incana* and *Symphoricarpos albus* were also common associates. The established range for *S. marilandica* is eastern North America, west to eastern British Columbia and southward along the Rocky Mountains. This collection may be the first record from Washington, although Hitchcock (1961) states that it probably occurs in extreme northeastern Washington.

Senecio jacobaea L. Fifteen km north of Winthrop, Okanogan County, elevation ca 79 m; *Naas & Naas 2347* (WI). This collection was made on an open flat in association with grasses, in a scattered pine (*Pinus ponderosa*) forest. Although this poisonous plant has become widely established in the United States and Canada and is known in western Washington, it had previously not been reported east of the Cascades in our state.

Senecio lugens Rich. (*S. glaucescens* Rydb.). Rock Mtn., Okanogan County; *Douglas & Douglas 4710* (GD). Monument 104 (U.S.-Canadian border), Okanogan County; *Douglas & Douglas 4540* (GD, NY). This species is extremely common from Alaska and the Yukon south in the Rocky Mountains to northern Wyoming. Although a disjunct population occurs in the Olympic Mountains of Washington, this taxon has not previously been reported from the Washington Cascades. It is a widespread but infrequent component of many of the drier alpine communities in the eastern North Cascades (Douglas, 1973). These collections were taken on dry alpine ridges at 2300-2400 m elevation. The Rock Mtn. collection was determined by G. G. Douglas and the Monument 104 collection was determined by A. Cronquist.

Thalictrum fendleri Englm. ex Gray. Eleven km north of Winthrop, Okanogan County, elevation ca 655 m; *Naas & Naas 2204* (FS, WI). Twenty-one km north of Winthrop, elevation ca 670 m; *Naas & Naas 2312* (FS, WI). The population from which collection 2204 was taken was growing in a damp ravine with *Populus tremuloides.* The population of collection 2312 was found in a *Picea engelmannii* forest. The previously established range of this taxon was the central and southern Rockies, west to Baja, California, and north to northeastern Oregon. These two collections represent the first records of this species in the State of Washington. Identifications were confirmed by Charles Feddema.

Torilis japonica (Houtt.) DC. One km northwest of Marblemount, Skagit County, elevation ca 104 m; *Naas & Naas 3438* (NC, WW). This tall, coarse umbel was well

established along a moist, gravelly stream bank in association with *Rubus spectabilis* and *R. parviflorus*. This is an introduced species which had previously been reported from southwestern Oregon and northwestern California (Abrams, 1951). Thus, this collection represents a new record for the State of Washington.

Vaccinium scoparium Leiberg (*V. myrtillus* var. *microphyllum* Hook.; *V. microphyllum* Rydb.; *V. erythrococcum* Rydb.). Skyline Divide, Mount Baker area, Whatcom County; *Douglas 2349* (GD). This collection was taken from the front of the northeast aspect of a solifluction lobe at an elevation of 1900 m. This species is prevalent throughout the Rocky Mountains and although it is also common in the subalpine and alpine zones of the eastern Cascades, this is the first record west of the Cascade Crest.

Veronica hederaefolia L. Two and one half km southwest of Coupeville, Island County, elevation ca 15 m; *Naas & Naas 1306* (SV, WW). This European introduction was common at this location in disturbed ground at the margin of a cultivated field. According to Hitchcock *et al.* (1959), this species had previously been known in our range from a single collection at Almota, Snake River Canyon, Whitman County, but Gaines and Swan (1972) state that it has recently become common in eastern Washington. It has also been recently collected at Bellingham, Washington (specimen at WW).

Literature Cited

Abrams, L. 1951. Illustrated Flora of the Pacific States. Vol. III. Stanford Univ. Press, Stanford, Calif. 866 pp.

Douglas, G. W. 1971. The alpine-subalpine flora of the North Cascade Range. Wasmann J. Biol. 29: 129-168.

————. 1973. Alpine plant communities of the North Cascade Range, Washington and British Columbia. (Dept. of Botany), Univ. of Alberta, Ph.D. thesis. 145 pp.

————, and L. C. Bliss. 1977. Alpine and High Subalpine Plant Communities of the North Cascades Range, Washington and British Columbia. Ecol. Monogr. 47 (in press).

————, D. Naas, and R. Naas. 1973. New plant records and ranges for Washington, Northw. Sci. 47: 105-108.

————, and R. J. Taylor. 1970. Contributions to the flora of Washington. Rhodora 72: 496-501.

Gaines, X. M., and D. G. Swan. 1972. Weeds of Eastern Washington and Adjacent Areas. C. W. Hill/Printers, Spokane, Wash. 349 pp.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1955. 1959, 1961, 1964, 1969. Vascular Plants of the Pacific Northwest. Vol. 1-5. Univ. of Wash. Press, Seattle, Wash.

Taylor, R. J., and G. W. Douglas. 1977. Plant ecology and natural history of Chowder Ridge, Mt. Baker: a potential alpine research natural area in the western North Cascades Northw. Sci. 52: 35-50.

————, G. W. Douglas, and L. M. Sundquist. 1973. Contributions to the flora of Washington. II. Northw. Sci. 47: 169-179.

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Food Habits of Rocky Mountain Whitefish (Prosopium williamsoni) from the Teton River in Relation to Their Age and Growth

Abstract

Food habits of Rocky Mountain whitefish (*Prosopium williamsoni*) were related to age classes. Three dominant families of food items in the diet of whitefish were Chironomidae, Hydroptilidae, and Dytiscidae. Chironomids occurred in all fish. The percent of chironomids in the diet decreased as the ages increased. Statistical analysis of diversity of food habits between age classes revealed significant differences, except between age class one and two, and age three and combined ages four and five, which may mean that within these subgroups fish could compete for food.

Introduction

The Rocky Mountain whitefish *Prosopium williamsoni* (Girard) is the most abundant species in many streams in western North America (Sigler and Miller, 1963; Brown, 1971; McPhail and Lindsey, 1970; Goodnight and Bjornn, 1971). Whitefish have been reported as competing with trout for food (Sigler, 1951). Current ecological thought is that direct competitors do not exist in the same environment (Royce, 1972). The subtle differences in space utilization and food utilization often prevent even members of the same genera from being in direct competition (Johnson and Minckley, 1972). Biological theory, therefore, indicates that whitefish and trout should not be in direct competition, yet examination of food habits of the species reveals similarities in diet (Carl *et al.,* 1959; Carlander, 1969). The interaction of whitefish and trout populations has not been clearly established (Baxter and Simon, 1970). Research into the biology of various trout and salmon species has been more extensive than the research into the biology of whitefish even though the whitefish may be the most abundant fish in many streams. Frequently, diets are not related to age classes, but merely to size categories of fish. This situation makes an accurate assessment of competition between whitefish, as well as between whitefish and trout, impractical. This study of whitefish in the Teton River relates food items to age class.

Description of Study Area

The study area was located in Teton County, Idaho, at an elevation of 1550 m. The fish collecting area was the entrance of Teton Creek into the Teton River. The area is a sparsely populated mountainous region characterized by hillsides with dry farms, aspen, and pine. The area is moderately grazed, and bank erosion was present. This

erosion has caused silting in both Teton Creek and Teton River, with heavier silting in the slower flowing Teton Creek.

Methods

Seventy-five whitefish were collected during October 1973 by electrofishing. Standard length, body depth, weight, and sex were recorded. Scale samples were taken from below the dorsal fin and above the lateral line. Back-calculated growth was determined by using a clear plastic nomograph (Lowry, 1951). Stomachs were removed, tied in cheese cloth, cross indexed with scales, and preserved in 10 percent formalin. Volumes of the stomachs were subsequently determined by displacement. Stomach contents were analyzed by separating and counting each individual organism under a variable power dissecting microscope. Classifications were based on taxonomic keys by Barnes (1963), Borror and Delong (1964), Ross (1956), Ward and Whipple (1918), and Needham and Needham (1966). The frequence of occurrence (FO%) was established for each food item (Lagler, 1956). The numerical method (N%) was also employed to establish percent of various food items in the diet (Lagler, 1956). The data obtained were then related to whitefish age classes. Shannon's index of diversity (Zar, 1974) was utilized to calculate diversity indices of food items for each whitefish age class. Indices of diversity were then compared by t-test to test the hypothesis that age classes have similar diets.

Two quantitative and two qualitative samples of aquatic organisms in the Teton River were taken by use of Hess net ($1/16m^2$) and kick net, respectively. The quantitative samples were taken at two locations representative of the study site. The total area sampled encompassed $1/8m^2$. The substrate consisted primarily of fine sand and silt, with water depth ranging from .6 to 1.5 m.

Forage ratio for each food item was calculated by dividing the percentage in stomach by the percentage in the quantitative environmental samples. Values higher than one indicate preferential selection, a value equal to one is interpreted as chance, and values less than one indicate avoidance.

Results

Age and growth are determined for 75 Rocky Mountain whitefish from the Teton River (Table 1). Figure 1 shows the percent of each food item present in the entire fish sample. The three dominant families of food items in the diet of whitefish were Chironomidae, Hydroptilidae, and Dytiscidae (Fig. 1). These families were compared by chi-square analysis to determine if there were differences in food items selected between age groups (Table 2). Quantitative aquatic invertebrate sampling indicated chironomid larvae as the most abundant, followed by tubificids (Table 3). Percent of individual food items (N%) and frequency of occurrence (FO%) of food items for the various age classes are listed in Table 4. Analysis of forage ratios by age classes revealed that chironomid larvae had a positive selection ratio in all age groups. Brachycentridae had a ratio less than one, indicating negative selection. Age class four and five had the highest occurrence of Brachycentridae. A positive selection for Hydrachinellidae was seen in age class three whitefish. Haliplidae had positive selection by age class three and a negative selection in all other age classes. Basommataphora's forage ratio for classes four and five revealed positive preference; forage ratio for this

organism in all other age classes indicated negative selection. Sphaeridae had chance selection in age class three and combined age classes four and five, and negative selection in age classes one and two.

Simuliidae did not show up in any aquatic samples (Table 3), but age class three indicated selection of Simuliidae as a food item. Dytiscidae was not collected in aquatic samples; however, it occurred in all age class stomachs, and was increasingly selected

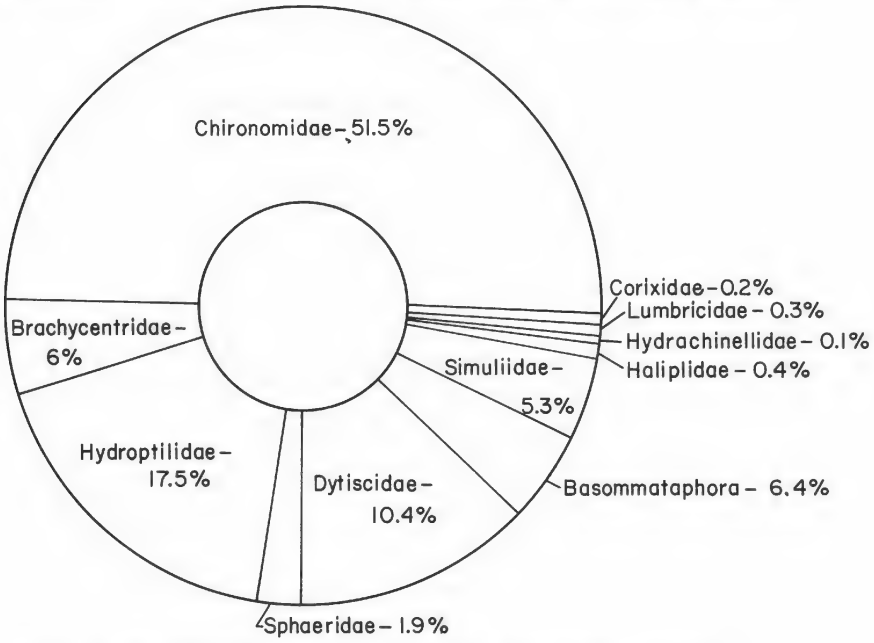

Figure 1. Percent of food items present in seventy-five Teton River mountain whitefish.

TABLE 1. Growth measurements of whitefish in Teton River for various age classes at time of capture.

Age Class	Sex	Sample Size	Average Standard Length (cm)	Average Weight (g)	Average Back-calculated Standard Length (cm at each annulus) 1	2	3	4	5	Average Depth (cm)	Average Condition Factor
1	—	16	10.50	14.65	6.50					2.20	0.0124
2	Males	15	17.00	86.50	6.96	13.20				3.74	0.0170
2	Females	7	14.78	84.78	6.74	13.00				3.85	0.0168
3	Males	18	18.10	92.69	5.86	9.82	14.99			4.14	0.0149
3	Females	4	21.25	143.12	8.87	13.12	18.50			4.40	0.0148
4	Males	9	23.60	193.20	6.22	11.61	16.90	21.00		5.08	0.0147
4	Females	1	25.00	233.00	7.00	10.50	17.00	23.00		5.10	0.0149
5	Males	2	26.25	251.50	6.50	9.50	14.00	19.00	24.00	5.45	0.0138
5	Females	3	28.60	370.00	6.83	11.40	17.06	21.50	25.83	6.53	0.0169
Average for Males					6.33	11.35	15.53	20.63	24.00		
Average for Females					7.34	12.55	17.77	21.92	25.83		
Average all Groups					6.57	11.66	16.01	20.98	25.10		
			Males			5.02	4.18	5.10	3.37		
			Females			5.21	5.22	4.15	3.97		
			All Groups			5.09	4.35	4.97	4.12		

for as age increased. Hydroptilidae larvae were not collected in the quantitative samples, but did appear as a major food item in the diet of the whitefish. These three families were probably picked up in the drift or missed by the sampling device. Additional environmental sampling is required to determine the distribution of these organisms.

Comparison of food habits between age classes revealed significant differences in diet between age classes (Table 2). No differences in food habits existed between age classes one and two. It appears that these age classes are dependent upon the same

TABLE 2. Chi-square test results for differences of selection between age groups of mountain whitefish on three dominant food item families and t-test results of comparisons of indices of diversity between age classes.

Food Item	Age Class Comparison	X^2 Value	$X^2.05(2)$ with 1 d.f.	Conclusion
Chironomidae	1 vs 2	2.28	3.841	similar selection
	2 vs 3	5.32	3.841	dissimilar selection
	3 vs 4-5	5.07	3.841	dissimilar selection
Hydroptilidae	1 vs 2	2.30	3.841	similar selection
	2 vs 3	1.19	3.841	similar selection
	3 vs 4-5	10.74	3.841	dissimilar selection
Dytiscidae	1 vs 2	6.44	3.841	dissimilar selection
	2 vs 3	6.33	3.841	dissimilar selection
	3 vs 4-5	1.86	3.841	similar selection

Comparison of Ages	Differences (J_1-J_2)	[s]H1-H2	t-value	[t].05(2)1	Conclusion	
1 vs 2	-0.1028	0.0600	-1.7133	1.973	Ho: $J_1=J_2$	Accept
1 vs 3	-0.4106	0.0574	-7.1533	1.973	Ho: $J_1=J_3$	Reject
1 vs 4-5	-0.4052	0.0539	-7.5176	1.972	Ho: $J_1=J_{4-5}$	Reject
2 vs 3	-0.3078	0.0640	-4.8094	1.972	Ho: $J_2=J_3$	Reject
2 vs 4-5	-0.3024	0.0608	-4.9737	1.973	Ho: $J_2=J_{4-5}$	Reject
3 vs 4-5	-0.0054	0.0583	0.0926	1.973	Ho: $J_3=J_{4-5}$	Accept

[s]H=Shannon's Index of Diversity.

TABLE 3. Quantitative and qualitative samples of aquatic organisms in the Teton River.

Taxon Present	Taxa present in two kick net samples of study area.	Percent of individual Taxa present in 1/8 m^2 of study area.
Arthropoda		
Trichoptera		
Hydroptilidae	+	0.0
Brachycentridae (larvae)	+	16.0
Diptera		
Chironomidae (larvae)	+	35.8
Plecoptera		
Acroneuriinae		2.0
Acarina		
Hydrachinellidae	+	2.0
Coleoptera		
Haliplidae **Haliplus** sp. (larvae)	+	0.5
Mollusca		
Pelecypoda		
Sphaeridae **Pisidium** sp.	+	12.8
Gastropoda		
Basommataphora **Physa** sp.	+	6.1
Annelida		
Oligochaeta		
Tubificidae	+	24.5

food resources. There was a significant difference in the indices of food diversity between age classes one and two and age class three indicating reduced competition for food. There was also a highly significant difference in food categories between age class one and combined age classes four and five. Age class three and combined age class four and five showed an insignificant difference between food categories and may be in competition for food.

TABLE 4. Percent of individual food items (N%) and frequency of occurrence (FO%) of food items for various age classes of Teton River whitefish.

Food Items	N% Age Class 1	FO% Age Class 1	N% Age Class 2	FO% Age Class 2	N% Age Class 3	FO% Age Class 3	N% Age Class 4&5	FO% Age Class 4&5
Chironomidae	85.8	100.0	78.5	78.3	50.4	77.0	45.3	53.3
Simuliidae	1.0	12.5	0.1	8.7	13.1	31.8	0.6	6.7
Brachycentridae	0.1	6.3	1.9	21.7	4.2	22.7	9.8	60.0
Hydroptilidae	12.6	81.3	9.9	34.8	10.9	31.8	21.5	26.6
Hydrachinellidae	0.0	0.0	0.0	0.0	0.2	9.0	0.0	0.0
Haliplidae	0.0	0.0	0.0	0.0	1.0	9.0	0.2	6.7
Dytiscidae	0.4	18.8	8.5	56.5	12.4	72.7	8.4	66.6
Basommataphora	0.1	18.8	0.7	8.7	4.8	27.2	11.2	33.3
Sphaeridae	0.0	0.0	0.1	4.3	2.7	22.7	2.3	20.0
Corixidae	0.0	0.0	0.2	8.7	0.0	0.0	0.2	6.7
Lumbricidae	0.0	0.0	0.0	0.0	0.1	13.6	0.6	13.3

Discussion and Conclusion

Food Habits

Whitefish food habits in the Teton River indicated variation in families of aquatic insects utilized between different age classes. Similar results were obtained from food habit studies of whitefish of Wyoming, British Columbia, and in the Snake River of Idaho (Baxter and Simon, 1970; Carl *et al.*, 1969; Carlander, 1969). This study is most nearly comparable to that of Snake River whitefish in Grand Teton National Park (Pontius and Parker, 1973).

The October 30, 1970 collection of Pontius and Parker (1973) of size class one whitefish from the Snake River is equivalent to age classes one-three in this study. They indicated chironomids in all stomachs of class one fish, and as the size classes increased, the percent of chironomids in the diet decreased. This study confirms these results. They found Plecoptera and ephemeropterans in Snake River whitefish, as did Sigler (1951) in Logan River whitefish, and as Laakso (1951) found in whitefish of Yellowstone River. However, the two orders appeared in small numbers in Laakso's (1951) fall samples. Plecoptera and ephemeropterans were not present in Teton River whitefish stomachs. Ephemeropterans were not collected in the aquatic samples of the Teton River, and a small percent of plecopterans were sampled. This finding may be a function of the siltation of Teton River. Tubificidae and chironomids were the most abundant organisms in the environmental samples and are characteristic of silt bottoms, but the numbers of Plecoptera and Ephemeroptera decrease in silt substrate (Eustis and Hillen, 1954). Teton River whitefish food habits may be adapted to the environmental disturbance resulting from overgrazed stream banks.

Food Diversity in Age Classes

Intraspecific competition for food items may exist between age class one and age

class two when food resources are limited. However, age class two had a highly significant selection for Dytiscidae compared to age class one. This difference probably results from the ability of the larger fish to feed on the large Dytiscidae larvae. Age class two had a reduced weight gain compared to the other age groups (Table 1). This disparity could result from competition for food. Age class two fish are less capable of competing with larger age classes and partially share their feeding niche with age class one.

Age class three whitefish were captured in all sampling areas and contained the same types of food items as age class four and five. However, age class four and five had a higher occurrence of larger food items in the stomach than did age class three. Age class three also showed less linear growth than age class four and five. This disparity again may result from intraspecific competition (Emlen, 1966). Age class three has to expend more energy collecting smaller food items than age class four and five, which feed on larger items.

Further study is needed in the biology of the whitefish. Studies in population dynamics, food habits, and growth need to be undertaken in conjunction with other salmonids during seasonal changes, low waterflows, and different habitat types. The interaction of whitefish and trout needs to be further understood so that management plans may be adequately constructed for the game fish species. The decrease in the more preferred trout species is probably the result of stream siltation and not intraspecific competition with whitefish. The abundance and believed increase in whitefish may be correlated with decreased trout densities which result from increased silt deposition. The whitefish may adapt more readily than trout to a silted environment.

Literature Cited

Barnes, R. D. 1963. Invertebrate Zoology. W. B. Saunders Company, West Washington Square, Philadelphia, Pa. 743 pp.

Baxter, G. T., and J. R. Simon. 1970. Wyoming Fishes. Bull. Wyoming Fish and Game Department, No. 4:34.

Borror, D. J., and D. M. Delong. 1964. Introduction to the Study of Insects. Holt, Rinehart and Winston, New York. 819 pp.

Brown, C. 1971. Fishes of Montana, pp. 44-45. The Endowment and Research Foundation. Montana State University. 207 pp.

Carl, G. C., W. A. Clemens, and C. C. Lindsey. 1959. The Freshwater Fishes of British Columbia, pp. 37-84. British Columbia Provincial Museum. Vancouver, B.C. No. 5, 3rd ed. 192 pp.

Carlander, K. D. 1969. Handbook of Freshwater Fishery Biology. Vol. 1. The Iowa State University Press, Ames, Iowa. 752 pp.

Emlen, J.M. 1966. The role of time and energy in food preference. Amer. Natur. 100: 611-617.

Eustis, A. B., and R. H. Hillen. 1954. Stream sediment removal by controlled reservoir release. Prog. Fish-Cult., 16: 30-35.

Goodnight, W. H., and T. C. Bjornn. 1971. Fish production in two Idaho streams. Trans. Amer. Fish. Soc. 100: 769-780.

Johnson, D. W., and W. L. Minckley. 1972. Variability in Arizona buffalo fishes. Copeia 1972: 12-17.

Laakso, Martin. 1951. Food habits of the Yellowstone whitefish *Prosopium williamsoni cismontanus* (Jordan). Trans. Amer. Fish. Soc. 80: 99-109.

Lagler, Karl F. 1956. Freshwater Fishery Biology. Wm. C. Brown Company, Publishers, Dubuque, Iowa. 421 pp.

Lowry, Edward M. 1950. A nomograph for rapid back-calculation of fish lengths. Prog. Fish-Cult., 12: 199-202.

McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fish. Res. Bd. Canada. Bull. 173: 381.

Needham, J. G., and P.R. Needham. 1962. A Guide to the Study of Freshwater Biology, pp. 21-31. (5th Ed.) Holden-Day, Inc., San Francisco. 108 pp.

Pontius, R. W., and M. Parker. 1973. Food habits of the mountain whitefish, *Prosopium williamsoni* (Girard). Trans. Amer. Fish. Soc. 102: 764-773.

Ross, H. H. 1956. A Textbook of Entomology. John Wiley and Sons, Inc., New York, London, Sydney. 539 pp.

Royce, W. F. 1972. Introduction to the Fishery Services, p. 126 (2nd. Ed.) Academic Press, Inc., New York. 351 pp.
Sigler, William F. 1951. The life history and management of the mountain whitefish (*Prosopium williamsoni*) (Girard) in Logan River, Utah. Utah State Coll. Exp. Sta. Bull. 347: 1-21.
————, and R. R. Miller. 1963. Fishes of Utah. Utah State Department of Fish and Game, Salt Lake City, Utah. 59 pp.
Ward, H. B., and G. C. Whipple. 1918. Freshwater Biology. John Wiley, New York. 1111 pp.
Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J. 620 pp.

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Black-tailed Deer (Odocoileus hemonius columbianus) and Forest Reproduction: Blake Island Marine State Park, Washington

Abstract

Using the pellet-group count method, I estimated that Blake Island Marine State Park supports about 105 black-tailed deer. The scarcity of seedlings, saplings, and pole-stage trees suggests that the overabundance of deer is severely limiting the forest regrowth of Blake Island.

Introduction

Blake Island Marine State Park encompasses 192 ha and lies 4.8 km west of Seattle in central Puget Sound, Kitsap County, Washington. The island is predominantly forested and offers seasonal camping and picnicking.

Much of the merchantable timber on Blake Island was first logged in the 1850s. Periodic fires later occurred, and in the early twentieth century the island became an estate under private ownership (Anonymous, 1973). Blake Island achieved present status in 1957 when it was acquired by Washington State Parks.

The plant community of Blake Island is similar to those occurring around Puget Sound and in the surrounding *Tsuga heterophylla* zone (Franklin and Dyrness, 1973). Precipitation is about 84 cm per year. Tree species in the overstory consist of *Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata,* and *Alnus rubra. Picea sitchensis, Abies grandis, Acer macrophyllum,* and *Arbutus menziesii* occur to a lesser extent. The understory is primarily *Urtica dioica, Rubus spectabilis, Gaultheria shallon, Polystichum,* and *Sambucus.*

Methods and Results

Although the shade-tolerant climax *Tsuga heterophylla* is capable of reproducing under a forest canopy (Franklin and Dyrness, 1973), very little natural forest regeneration is evident on Blake Island. Close examination of 220 sample plots, 2.4-m in diameter, revealed a total of only 23 tree seedlings. The majority of these seedlings were *Tsuga heterophylla* and were less than 5 cm in height. In addition, general observation shows that a few sitka spruce and Douglas-fir have become locally established where dense salal inhibits browsing by deer. If one discounts the occasional tall thickets of salmonberry, the vertical zonation of vegetation present on the island is simplified; i.e., it consists of a relatively mature forest overstory and a heavily browsed shrub understory.

Park personnel are cognizant of the problem and in spring 1975, 800 *Pseudotsuga menziesii, Abies grandis,* and *Abies procera* were planted in an opening on the southeast side of the island. Soon after, browsing pressure by black-tailed deer accounted

for high mortality among the seedlings. In the early spring of 1976 a sample from the remaining seedlings showed 87 percent had the terminal bud "nipped-off" and many lateral branches were browsed as well. The tallest unbrowsed seedlings were about 15 cm in height.

The size of the black-tailed deer population was estimated using the pellet-group count method (Giles, 1971). Two hundred and twenty-eight randomly spaced 2.4-m diameter plots were established and cleared of pellet groups in December, 1975. Examination of the plots 48 days later revealed a total of 165 pellet groups—yielding an estimate of 119 deer. The plots were cleared and checked again 63 days later. An early spring growth of nettles made pellet groups more difficult to observe in the April count. One hundred and fifty-two groups were counted for 216 plots recovered —yielding an estimate of 90 deer. An average of winter 1975 and spring 1976 estimates revealed a density of 105 deer for the 192 ha island (one deer per 1.8 ha or the equivalent to 365 deer per sq km).

Discussion

Severe browsing pressure by black-tailed deer is limiting the forest regrowth of Blake Island. Park personnel report an overabundance of deer for at least seven years, and the gap in the progression of size classes in the stand further supports the hypothesis that the high deer density has long existed.

Graham (1954) shows that browsing by white-tailed deer has produced changes in the composition of the forest which are undesirable for the best management of timber. Hines (1963) in an Oregon study found that the percentage of Douglas-fir seedlings browsed by deer rose as the density of deer increased: at 73 deer per sq km only 2 percent of the seedlings were damaged, but at 210 deer per sq km 45 percent of the seedlings were damaged. Studies by Bartlett (1958), Bennet (1962), Graham (1954), Grange (1949), and Stoeckler *et al.* (1957) of damage to forest reproduction by white-tailed deer show slight damage of levels of about 52 deer per sq km; it increases rapidly up to 285+ deer per sq km, at which point relative damage is described as total.

Hines (1963) found that in Oregon small seedlings escaped being browsed in winter since they, along with other low forage, are covered by snow. The fact that Blake Island rarely has snow cover may partly explain why small seedlings are so vulnerable.

If the present situation is continued indefinitely, probably the present forest will mature and die without replacement. Since this outcome is not desired by the Washington State Parks Administration, the suggestion of remedial action is in order. Two possible courses of action are the establishment of exclosures and the reduction of deer density. If exclosures are built, they can be removed when the seedlings have grown beyond reach (i.e., over 122 cm tall). If deer are reduced in density, they should presumably be kept at about half the present population, or about 50 deer total, until forest regeneration has grown beyond their reach. These measures will help ensure that Blake Island State Park has both forest and deer for future enjoyment.

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Literature Cited

Anonymous. 1973. "Facts about Blake Island." Washington State Parks. 1 p.
Bartlett, C. O. 1958. A Study of Some Deer and Forest Relationships in Rondeau Provincial Park. Ontario Dept. Lands and Forests, Biol. Serv. 66. 137 pp.
Bennet, A. L. 1962. Industrial Forestry and Wildlife—The Northwest. J. Forestry. 60(1): 118-120.
Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. Pacific Northwest Forest and Range Exper. Sta. U.S. For. Serv., Portland, Or. 417 pp.
Graham, S. A. 1954. "Changes in Northern Michigan Forests from Browsing by Deer." Trans. N. Amer. Wildl. Conf. 19: 526-533.
Giles, R. H. 1971. Wildlife Management Techniques. The Wildl. Soc., Wash., D.C. 633 pp.
Grange, W. 1949. The Way to Game Abundance; with an Explanation of Game Cycles. Scribner, New York. 365 pp.
Hines, W. W. 1963. "Relationships of Black-tailed Deer Density to Conifer Survival." Proc. Western Assoc. of State Game and Fish Comm. 43: 189-192.
Stoeckler, J. H., R. O. Strothmann, and L. W. Krefting. 1957. "Effects of Deer Browsing in Northern Hardwood-Hemlock Type in Northeastern Wisconsin." J. Wildl. Mgt. 21(1): 75-80.

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Coelozoic Myxosporida of Fishes of Western Montana: Genus Chloromyxum

Abstract

Coelozoic infections of *Chloromyxum* (Myxosporidea: Chloromyxidae) are reported from fishes of the Columbia drainage in Western Montana. Infections of *C. trijugum* Kudo were found in the gall bladders of 18 of 31 pumpkinseeds (*Lepomis gibbosus*). *Chloromyxum wardi* Kudo was found in the gall bladders of the four salmonids, *Salmo clarki*, *S. gairdneri*, *Salvelinus fontinalis*, and *S. malma*. Descriptive notes, evidence of host specificity, and discussion of possible affinities of these parasites are provided.

Introduction

The protozoan order Myxosporida includes important fish pathogens, yet only a single published study lists myxosporidan infections from fishes of the Columbia drainage of western Montana (Mitchell, 1967).

The present report is of infections of two gall bladder infecting species of *Chloromyxum* seen during a survey of fishes conducted in western Montana from 1965 through 1968. As discussed by Lom (1961), most species descriptions of Myxosporida do not adequately represent variations in the parasites and are often based on composite drawings of so-called type specimens. Thus, to facilitate future recognition of these parasites, descriptive notes and diagnostic photomicrographs are presented which supplement previous records of natural variability.

Methods and Materials

Fish were obtained by angling, seining, and gill netting. Collections were made from the Bitterroot, Clark Fork, Clearwater, and Flathead rivers and their major tributaries; from Fish, Flathead, Loon, and Placid Lakes; and from many small impoundments in western Montana. All specimens were examined within a few hours of death. Most were killed and examined immediately. Representatives of all fish species found in western Montana except members of the Ictaluridae and Gadidae were examined. Collections of specimens of the catostomid, cyprinid, and salmonid fishes were made during all seasons. Trophozoites and spores were examined in wet mounts of saline-diluted body fluids.

Results

Two coelozoic species of the genus *Chloromyxum* were found, both occurring in the gall bladders. The fishes examined and percentages of infection are presented in Table 1.

TABLE 1. **Chloromyxum** infections in fishes of western Montana.

Fishes Examined	No. Examined	No. Infected	%	Species of Chloromyxum
Catostomus catostomus	75	0	0	
Catostomus macrocheilus	133	0	0	
Cottus cognatus	3	0	0	
Esox lucius	15	0	0	
Gambusia affinis	12	0	0	
Lepomis gibbosus	31	18	58	Chloromyxum trijugum
Micropterus salmoides	9	0	0	
Mylocheilus carinus	10	0	0	
Oncorhynchus kisutch	2	0	0	
Oncorhynchus nerka	2	0	0	
Perca flavescens	4	0	0	
Prosopium coulteri	60	0	0	
Prosopium williamsoni	49	0	0	
Ptychocheilus oregonensis	38	0	0	
Rhinichthys cataractae	12	0	0	
Richardsonius balteatus	40	0	0	
Salmo clarki	14	1	7	Chloromyxum wardi
Salmo gairdneri	55	16	29	Chloromyxum wardi
Salmo clarki X Salmo gairdneri	5	0	0	
Salmo trutta	5	0	0	
Salvelinus fontinalis	7	1	14	Chloromyxum wardi
Salvelinus malma	8	1	13	Chloromyxum wardi
Thymallus arcticus	5	0	0	
TOTAL	594	37	6	

Chloromyxum trijugum Kudo, 1919

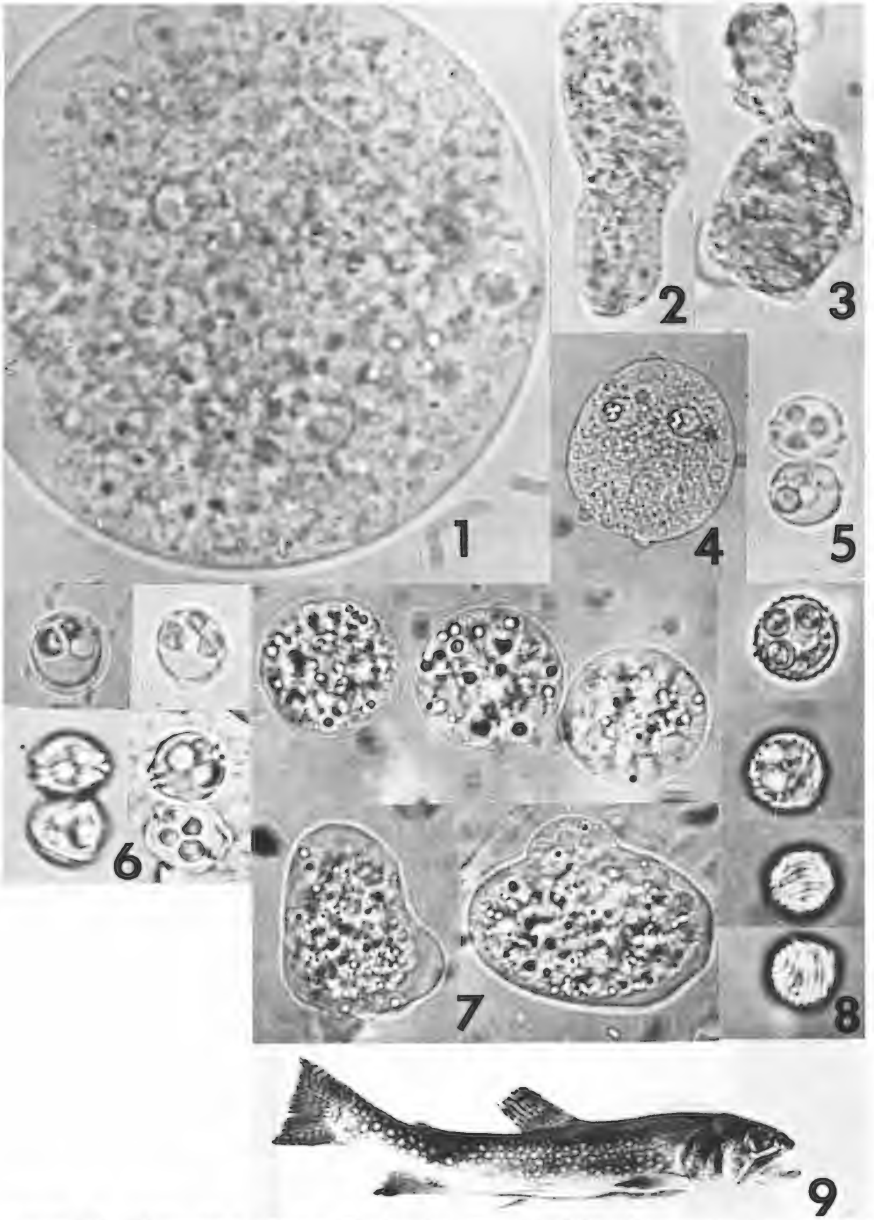
This comparatively well-known species has been reported from the gall bladders of several species of the family Centrarchidae (Jameson, 1931; Kudo, 1919, 1920; Meglitsch, 1937; Otto and Jahn, 1943).

Trophozoites and spores were found in the gall bladders of 18 of 26 mature specimens of *Lepomis gibbosus* from western Montana. Fishes were found infected in October, March, and July. The infected adult hosts were taken from seven impoundments; a single infected adult pumpkinseed was also obtained from the National Fish Hatchery in Miles City, Montana. Five juvenile pumpkinseeds taken from the Bitterroot and Clearwater rivers were not infected. No other species of fish in western Montana, including the closely related largemouth bass, *Micropterus salmoides,* has been found to harbor this parasite. Adult specimens of largemouth bass and 12 other species of fishes were collected from one or more of the impoundments which contained infected specimens of the pumpkinseed.

Trophozoites (Figures 1-5)

Previous reports indicate that the trophozoite is typically amoeboid, mono-, di-, or polysporous, and highly variable in size and shape.

Infections in *Lepomis gibbosus* in western Montana showed only polysporous trophozoites. Immature forms were generally spherical (Figs. 1 & 4). Sporulating trophozoites were generally elongate, irregular in outline and often lobopodate. Both mono- and disporous sporonts were observed. In the more common disporous forms (Fig. 5), the spores are typically in contact on nonsutural surfaces, and the sutural ridges lie at approximately right angles to the long axis of the sporont. Plasmotomy



Figures 1-4. *Chloromyxum trijugum.* Trophozoites. Figure 1. Spherical presporous form showing differentiation of ecto- and endoplasm, X 1500. Figures 2, 3. Elongate presporous forms; Figure 3. Trophozoite undergoing plasmotomy, X 650. Figure 4. Spherical form with monosporous sporonts, X 450. Figure 5. *Chloromyxum trijugum.* Disporous sporont, X 1500. Figure 6. *Chloromyxum trijugum.* Unstained spores, X 1500. Figure 7. *Chloromyxum wardi.* Unstained immature trophozoites, X 1000. Figure 8. *Chloromyxum wardi.* Unstained spores showing patterns of extrasutural ridges, X 1500. Figure 9. Emaciated brook trout infected with *Chloromyxum wardi*, X 0.2.

was observed in both presporous and sporulating trophozoites (Fig. 3). Sporulation occurs simultaneously throughout the trophozoites. Differentiation into distinct ecto- and endoplasm was variable (Figs. 1-4). Dimensions of trophozoites were within the ranges previously reported.

Spores (Fig. 6).

Spores observed in *Lepomis gibbosus* in western Montana were very similar to those described previously. Spores were generally spherical or subspherical in front view and broadly ovoid in side view. The sutural ridge was straight or slightly sinuous, thick, raised, and paralleled on both sides by a slightly lower ridge so that three ridges circled the sutural line. Kudo (1919) described 8 to 12 short ridges running toward the center of each valve from the sutural ridges in spores stained with iron hematoxylin or Giemsa's. Such ridges have not been mentioned by subsequent authors and I have not seen them on fresh spores. The four cnidocysts, as previously described, were equal or of slightly different sizes and were pyriform or spheroid with short fine anterior tips entering separate foramina. The coiled filament was generally invisible. Mature spores in sporont envelopes often showed a hyaline mucoid caudal process or envelope.

The following dimensions were recorded from nine specimens of *L. gibbosus* in western Montana: 8.0-11 μm (avg of 50: 9.6) x 8.0-9.5 μm (avg of 53: 9.0) x 6.5-9.6 μm (avg 25: 7.5); cnidocysts: 1.5-5.0 μm (avg of 22: 3.2).

Identification and Discussion

The spores and trophozoites found in *L. gibbosus* in this study were similar to those previously described. Dimensions of the spores seem to fit previous listings for *C. trijugum,* although this is the first record of ranges of variation in spore populations from several hosts. The occurrence of plasmotomy in trophozoites has been suspected (Kudo, 1919), but not previously recorded. Sporonts have not been previously described.

One other species of *Chloromyxum, C. gibbosum*, Herrick, 1941, has been described from the gall bladder of *Lepomis gibbosus.* This species has one sutural ridge per valve surrounding a deeply indented sutural line and may be distinguished from *C. trijugum* on this basis. *C. gibbosum* was described from pumpkinseeds in Lake Erie.

C. trijugum exhibits marked host specificity. To date this parasite has not been reported from fishes other than certain members of the Centrarchidae. *Micropterus salmoides,* a centrarchid that coinhabits waters of western Montana with *L. gibbosus,* does not appear to harbor this myxosporidan. *C. trijugum* was probably introduced into western Montana with its host.

Kudo (1919) noted that unlike most myxosporidans, infections of *C. trijugum* do not seem to be correlated with disease symptoms; no pathologic effects were noted in the Montana hosts.

Chloromyxum wardi Kudo, 1919

Infections were first described from the gall bladder of sockeye salmon, *Oncorhynchus nerka,* in Alaska. Also, Hoffman (1967) lists an unpublished record of *C. wardi* from the gall bladder and intestine of salmonids in the state of Washington. The original description by Kudo was made from a single preserved host. Shulman and Shtein (1962) report infections from sockeye salmon in Kamchatkan waters. Infections have

been found in four salmonid species taken from Placid and Fish Lakes in Missoula County, Montana (Table 1). These are all new host records for this parasite. Infected specimens were taken only from these two lakes. Specimens of these salmonids collected from other lakes and rivers were not infected. No other species of fish was found to harbor this parasite. Specimens of two other salmonids, the mountain whitefish (*Prosopium williamsoni*) and the coho salmon (*Oncorhynchus kisutch*), collected from Placid Lake were not infected. A single specimen of *Salmo gairdneri* from Placid Lake harbored infections of *C. wardi* and the digenetic trematode, *Crepidostomum farionis*, in the gall bladder.

Trophozoites (Fig. 7).

Previous reports are not complete. The two illustrations provided by Kudo (1919) were drawn from preserved material. As indicated by previous reports, trophozoites are highly variable. Immature forms (Fig. 7) may be spherical or irregular and amoeboid. Contrary to previous reports, differentiation of ecto- and endoplasm appears to vary considerably in the immature forms. All trophozoites observed in the Montana hosts were colorless. Sporulating forms possessed from two to five spores. Trophozoites with three spores were most common. Sporonts were monosporoblastic. The Montana forms fit the size range reported by Shulman and Shtein (1962).

Spores (Fig. 8).

This species is distinguished primarily by the surface architecture of the spore. The sutural ridge is raised and distinct, characteristically sinuous, and surrounded by ridged striations which course around the valves in converging patterns. These features are illustrated in hand drawings of Kudo (1919)and Shulman and Shtein (1962) and are evident in Figure 8. The patterns of striations and the nature of the sutural ridge were variable in the present study. In contrast to previous reports of the typical condition, the sutural ridge of many spores was straight and surrounded on either side by parallel striae. Cnidocysts were typically pyriform or spherical and of unequal size. The coiled filaments were not usually well defined; a single cnidocyst was seen with five coils.

Dimensions of fresh spores from five specimens of *Salmo gairdneri* in western Montana were: diameter in front view 9-12 μm (avg of 35: 10.6); diameter in sutural view 12 μm (13 measured); cnidocysts 3-4.5 x 2-3.5 μm (avg of 10: 3.2 x 2.2).

Identification and Discussion

The trophozoites and spores seen in western Montana closely match the previous descriptions of *C. wardi,* although this species is considerably more variable in both size and shape than previously reported.

The apparent limited distribution of *C. wardi* in western Montana may indicate that this parasite requires special limnological conditions which are not common in the area. Possibly *C. wardi* has only recently been introduced into the region, presumably via cultured trout. Some interspecific interaction may occur between *C. wardi* and the trematode, *Crepidostomum farionis. C. farionis* is widely distributed in salmonids in the Pacific Northwest including western Montana (Hoffman, 1967). The gall bladders of eight rainbow trout taken from Placid Lake were found infected with *C. farionis.* Only one of these was also infected with *C. wardi.* This finding may indicate some

negative influence of the trematode on populations of this myxosporidan, and may help explain the limited distribution of *C. wardi.*

Several species of *Chloromyxum* described from salmonids closely resemble *C. wardi.* Yasutake and Wood (1957) described a striated *Chloromyxum, C. majori,* from glomeruli of salmonids in the state of Washington. *Chloromyxum majori* was distinguished from other species of the genus primarily on the basis of site of infection. Léger (1906) described a similar species, *Chloromyxum truttae,* from the gall bladder and cystic duct of brown trout (*Salmo trutta*) in Dauphine, France. Shulman and Shtein (1962) list infections of *C. truttae* in brook trout (*Salvelinus fontinalis*) in the Leningrad region, and Davis (1947) found this species in brook trout in Vermont. The original description of *C. wardi* by Kudo was made from a single preserved host and no comparison with *C. truttae* was offered. The major distinction between *C. truttae* and *C. wardi* is reported to be in the patterns of extrasutural striations on the valves. Unlike the parallel striations of *C. truttae,* those of *C. wardi* course around the valves in various converging complex patterns (Shulman and Shtein, 1962). Additional studies on spore variability are required to test the validity of this distinction. Some variation in the striations on spores was noted in the present study.

Heavy infection by *C. truttae* has been associated with acute swelling and hyperemia of the gall bladder, loss of appetite, severe emaciation, and death in cultured brook trout in the U.S.S.R. (Shulman and Shtein, 1962). Although infections of *C. wardi* have not been associated with similar disease symptoms, the infected brook and rainbow trout in the present study were in poor condition. A single infected brook trout (Fig. 9) from Fish Lake was extremely emaciated. However, all of the infected rainbow trout from Placid Lake were also infected with leeches (*Piscicola* sp.), parasitic copepods (*Salmincola* sp.), and tapeworm plerocercoids (*Diphyllobothrium* sp.).

Relatively few myxosporidans have been associated with feral epizootics. The majority of severe myxosporidan epizootics have occurred under hatchery conditions that allow cumulative hyperinfection of hosts. Thus the potential economic significance of feral infections is that they may constitute reservoirs of domestic disease agents.

Literature Cited

Davis, H. S. 1947. Care and diseases of trout. Fish and Wildlife Research Rep. No. 12: 1-98.

Herrick, J. A. 1941. Some myxosporidian parasites of Lake Erie fishes. Trans. Amer. Micros. Soc. 60(2): 164-170.

Hoffman, G. L. 1967. Parasites of North American Freshwater Fishes. Univ. of California Press, Berkeley and Los Angeles. 486 pp.

Jameson, A. P. 1931. Notes on California Myxosporidia. J. Parasitol. 18(2): 59-68.

Kudo, R. R. 1919. Studies on Myxosporidia. A synopsis of genera and species. Ill. Biol. Monographs 5: 1-265.

———. 1920. Cnidosporidia in the vicinity of Urbana. Trans. Ill. State Acad. Sci. 18: 298-303.

Léger, L. 1906. Myxosporidies nouvelles, parasites des poissons. I. Sur une nouvelle maladie myxosporidienne de la truite indigène. Ann. Univ. Grenoble 18: 267-270.

Lom, J. 1961. Protozoan parasites in Czechoslovakian fishes. I. Myxosporidia, Suctoria. Zool. Listy 10: 45-58.

Meglitsch, P. A. 1937. On some new and known Myxosporidia of the fishes of Illinois. J. Parasitol. 23(5): 467-477.

Mitchell, L. G. 1967. *Myxidium macrocheili* n.sp. (Cnidospora: Myxidiidae) from the largescale sucker, *Catostomus macrocheilus* Girard, and a synopsis of the *Myxidium* of North American freshwater vertebrates. J. Protozool. 14(3): 415-424.

Otto, G. R., and T. L. Jahn. 1943. Internal myxosporidian infections of some fishes of the Okoboji region. Proc. Iowa Acad. Sci. 50: 323-335.

Shulman, S. S., and G. A. Shtein. 1962. Phylum Protozoa. Pp. 7-196. *In* Key to Parasites of Freshwater Fish of the USSR. I. E. Bykovskaya-Pavlovskaya *et al.* eds. Akad. Nauk SSR, Moscow-Leningrad. (Israel Program for Scientific Translations. 1964. OTS. U.S. Dept. of Commerce).
Yasutake, W. T., and E. M. Wood. 1957. Some Myxosporidia found in Pacific Northwest salmonids. J. Parasitol. 43(6): 633-642.

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Observations on the Diets of *Rana pretiosa*, *Rana pipiens*, and *Bufo boreas* from Western Montana

Abstract

Observations were made on the activities of feeding and habitat utilization of *Rana pretiosa* and *Rana pipiens* in Western Montana. Stomach samples from 50 *R. pretiosa* and 52 *R. pipiens* were analyzed. The diets were similar in taxonomic composition but varied in the dependence upon the taxa. The 40 families of insects and a variety of other organisms in the diets included ground-dwelling, foliage-feeding, and flying forms. Stomach samples from seven *B. boreas* contained primarily ground-dwelling forms.

Introduction

The diets of *Rana pretiosa* (Spotted frog), *Rana pipiens* (Leopard frog), and *Bufo boreas* (Boreal toad) have been studied in other parts of their respective ranges (Kelby, 1945; Linzey, 1967; Moore and Strickland, 1954, 1956; Turner, 1960; Whitaker, 1961; and Campbell, 1970), but have received little attention in the mountainous sections of western Montana.

Black discussed the distributional patterns of the genus *Rana* (Black, 1969) and the genus *Bufo* (Black, 1971) in Montana. The physiography of western Montana was also discussed by Black (1969).

The purpose of the present study was to examine the diets of *Rana pretiosa* and *Rana pipiens* from the Northern Flathead Valley, Montana. Lesser emphasis was placed on the diet of *Bufo boreas*.

Methods

Specimens were observed and collected at 14 riparian localities (Table 1) in the Flathead Valley during June, July, and the first week of August, 1974.

General activities of feeding and habitat selection were noted for each species. The habitats which were frequented by the ranids as well as those which were avoided were measured for height and density of the vegetation.

Only those specimens which contained food material were sacrificed. The number of members of each taxon of food items was recorded.

Results

Observations of the feeding behavior of the anurans indicated that they selected food items which were moving. Unsuccessful attempts to feed on an insect resulted in the ingestion of plant material or debris.

The habitats which were utilized by the ranids were similar in height and density of vegetation (Fig. 1). The available habitat varied from no vegetation to over 3000

stalks per square meter. The height of the grasses ranged to more than 2 m. Both frogs avoided sections of vegetation which contained more than 2000 stalks per square meter and which were more than 1 m in height. The excluding effect of density was reduced in grasses less than 15 cm in height. The excluding effect of height was reduced when the density was below 700 stalks per square meter. The diameter of the grasses ranged from 0.1 cm to 1.0 cm; mean approached 0.4 cm.

TABLE 1. List of sites, loci,[1] and resident species utilized in the study.

Location	Loci	Resident Species
Jette Pond	T23N, R21W, S2	1, -, 3
Jette Lake	T23N, R21W, S14	-, 2, 3
Roger's Lake	T27N, R27W, S30	1, 2, 3
Mud Lake	T31N, R19W, S9	1, 2, 3
Smith Lake	T27N, R22W, S7 & 9	-, 2, 3
Lion Lake	T30N, R19W, S9 & 16	1, -, 3
Ranch Slough	T31N, R19W, S21	-, 2, -
Morning Slough	T29N, R20W, S3	-, 2, -
Spoon Lake	T31N, R20W, S3	1, -, 3
Telephone Bog	T31N, R20W, S2	1, -, -
MacWenneger Slough	T29N, R20W, S31	-, 2, -
Skaggs Lake	T31N, R25W, S22 & 27	1, -, -
Doris Creek	T29N, R19W, S1	-, 2, -
Halfmoon Creek	T30N, R21W, S2	1, -, -

1 **Rana pretiosa**
2 **Rana pipiens**
3 **Bufo boreas**

[1]from U.S. Department of Agriculture, Forest Service, Map: Flathead National Forest (north half).

Rana pretiosa was not found more than 10 m from the edge of water (Fig. 2). Adults sat in shallow water or near the margin of the water. Juveniles were noted foraging further away from water than the adults.

Rana pipiens was not found more than 20 m from the edge of water (Fig. 2): both adults and juveniles were observed at various distances from the water.

Only two sites were found to be coinhabited by the ranids. Temporal separation occurred between the ranids at Mud Lake and, to a lesser extent, at Roger's Lake. Analysis of samples from the stomachs of 50 *Rana pretiosa* and 52 *Rana pipiens* illustrated that the frogs fed primarily upon the same food items (Table 2).

The presence of 40 families of insects and a variety of other organisms in the diet demonstrated the versatility of the feeding behavior of the frogs. Ground-dwelling insects, foliage-dwelling insects, and flying insects in the samples indicated that the frogs fed opportunistically.

The composition of the samples confirmed that the frogs fed primarily in the riparian habitat but occasionally fed in bordering meadows and woodlands. This behavior was supported by repeated observations.

Samples from the stomachs of seven *Bufo boreas* illustrated that the toads fed upon ground-dwelling insects (Formicidae and Carabidae) (Table 2). All samples contained Formicidae and pine needles plus other ground debris. Two samples contained only Formicidae and debris.

Discussion

The variety of dietary items which were represented by only one or two specimens from a family resulted from variations in the habitats which surrounded the 14 collection

sites and the associated insect fauna. Oliver (1955) placed emphasis upon the individual situation to account for variation in the composition of samples.

Repeated observations of the frogs confirmed that both fed upon any item which was of appropriate movement. The size of the item executed limited effect upon selection but did limit ingestion. Turner (1960) found that among *Rana pretiosa* juvenile frogs fed upon small prey but that adults ingested large and small prey. An analogous situation existed for *Rana pipiens*. Adult leopard frogs consumed Aeschnidae, Libellulidae, and newly metamorphosed toadlets, whereas juveniles did not. Juveniles were observed to attempt to consume the odonates, but all attempts failed before ingestion.

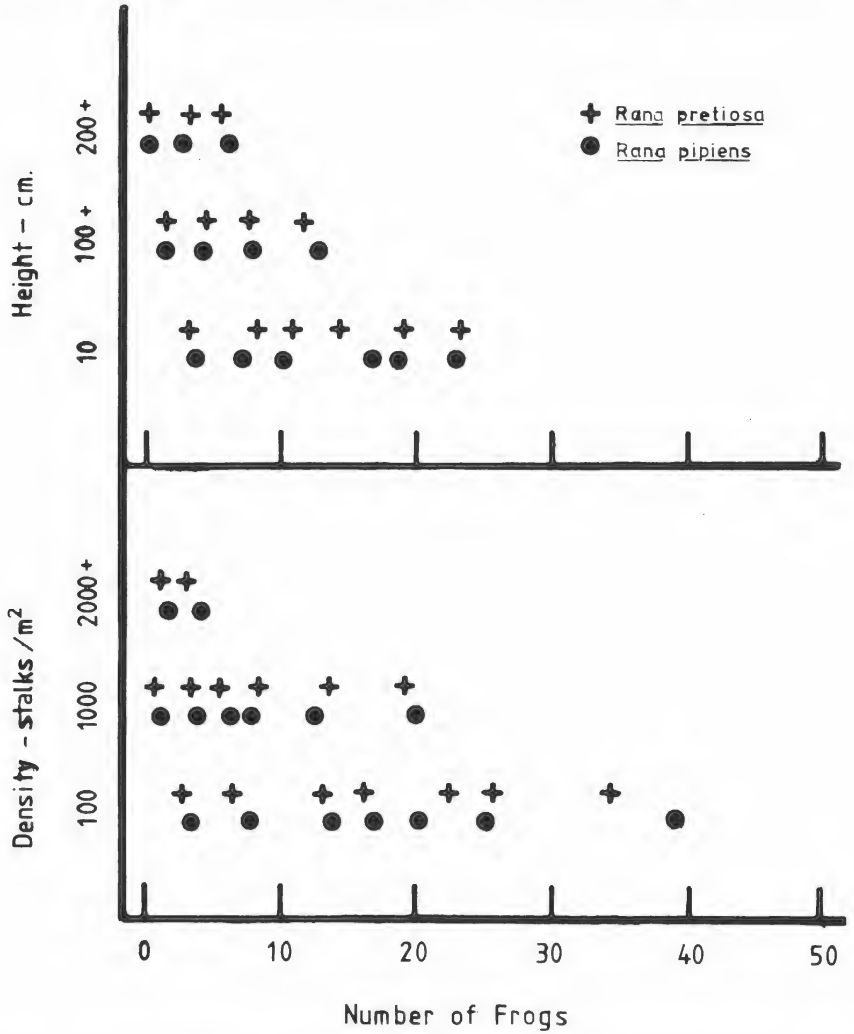

Figure 1. The relationship of the number of frogs to the height and to the density of the vegetation.

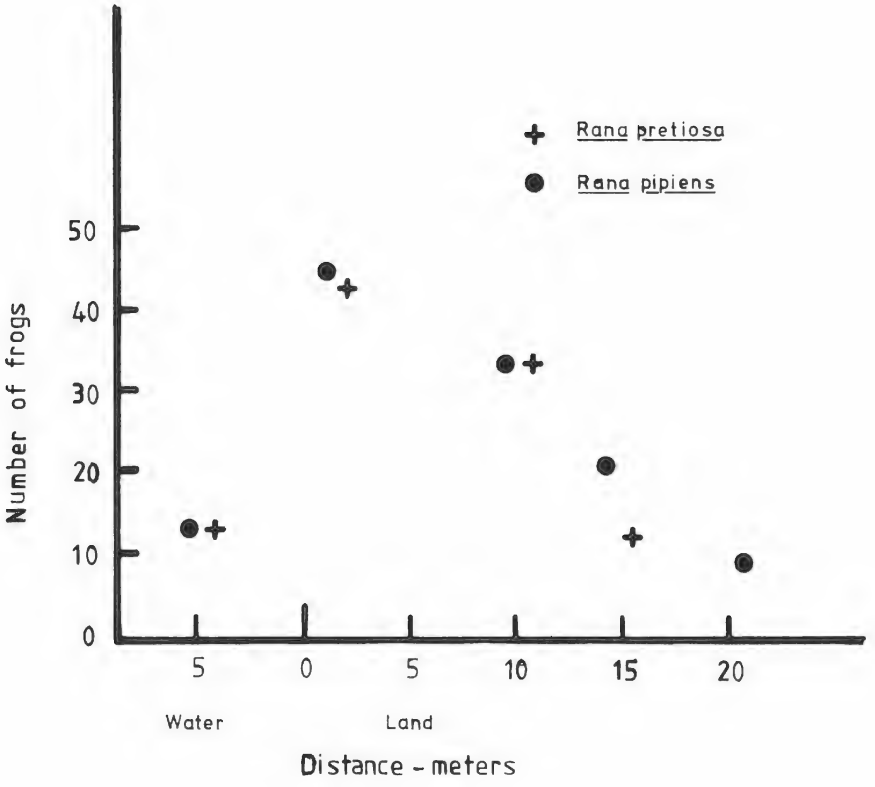

Figure 2. Location of frogs in relation to distance from water.

Whitaker (1961) and Turner (1960) demonstrated that abundance and availability of prey affects the diet. Abundance was dependent upon the life cycle of the prey (Linzey, 1967; Whitaker, 1961); availability was determined by the co-utilization of a habitat by prey and predator.

The consumption of 40 Coenagrionidae by *Rana pipiens* resulted from the abundance and availability of the dragonflies. The odonates were abundant along the margin of Smith Lake in mid-July which is the time of emergence. The odonates were available to the frogs because the vegetation in the area frequented by the frogs and dragonflies was short and thus brought the two physically close. Individual frogs were found to contain one, two, or three dragonflies along with other food items. No frog contained odonates exclusively.

Linzey (1967) reported that one or more families of insects form a stable portion of the diet. Carabidae, Chrysomelidae, and Tenebrionidae formed the major portion ($\sim$35 percent) of the diet of each ranid throughout the period of collection.

The diet of *Bufo boreas* as illustrated by this study did not differ in principle from the diet reported from other parts of the range (Campbell, 1970; Moore and Strickland,

TABLE 2. Comparison of ingested matter excluding inorganic and vegetable matter in selected specimen of Anura from northwestern Montana.

Food Item	R. pretiosa N = 50		R. pipiens N = 52		B. Boreas N = 7	
	No.	%	No.	%	No.	%
INSECTA						
Coleoptera		34.8		35.3		23.3
Cantharidae	7		3		-	
Carabidae	76		39		66	
Chrysomelidae	14		31		2	
Cicindelidae	10		1		1	
Coccinellidae	3		2		-	
Curculionidae	18		6		18	
Dytiscidae	3		1		1	
Elateridae	4		2		4	
Haliplidae	1		-		-	
Histeridae	1		-		-	
Meloidae	1		-		-	
Scarabaeidae	2		7		-	
Silphidae	-		7		1	
Staphylinidae	4		11		1	
Tenebrionidae	20		16		21	
Unidentified	13		5		-	
Diptera		9.2		11.3		0.4
Anthomyiidae	-		2		-	
Calliphoridae	11		-		-	
Chironomidae	5		18		-	
Dolichopodidae	-		6		-	
Muscidae	4		3		1	
Simuliidae	5		2		-	
Syrphidae	2		1		-	
Tipulidae	15		8		1	
Unidentified	4		2		-	
Hemiptera		5.0		4.5		-
Gerridae	18		7		-	
Miridae	3		2		-	
Nepidae	1		-		-	
Pentatomidae	1		1		-	
Reduviidae	2		-		-	
Saldidae	1		5		-	
Homoptera		0.4		0.5		-
Cercopidae	1		1		-	
Cicadellidae	1		-		-	
Membracidae	--		1		-	
Hymenoptera		22.4		9.7		75.3
Apidae	4		3		-	
Bombidae	1		-		-	
Formicidae	100		23		372	
Ichneumonidae	-		1		-	
Megachilidae	1		1		-	
Sphecidae	2		5		1	
Vespidae	7		3		-	
Lepidoptera		4.6		1.9		0.6
Adult	2		-		-	
Larvae	22		7		3	
Odonata		1.7		13.8		-
Aeschnidae	-		4		-	
Coenagrionidae	9		40		-	
Libellulidae	-		7		-	
Orthoptera		1.7		4.3		0.4
Acrididae	1		11		2	
Gryllacrididae	1		-		-	
Tetrigidae	7		5		-	
Plecoptera	2	0.4	2	0.5	-	-
Trichoptera	4	0.7	3	0.8	-	-

TABLE 2—Continued

Gastropoda	22	4.2	16	4.3	-	-
Arthropoda						
Arachnoida		14.5		11.6		3.0
Acarina	2		1		-	
Araneida	68		42		13	
Opiliones	4		2		2	
Chilopoda	-	-	1	0.2	-	-
Diplopoda	-	-	-	-	-	-
Julida	-	-	2	0.5	3	0.6
Amphibia						
Salientia						
Bufonidae	-		4	1.1	-	-
Total	517	100	373	100	513	100

1954). *Bufo boreas* fed upon such ground-dwelling forms as Formicidae, Carabidae, and Araenida. However, dependence upon specific taxa did vary. The apparent dependence upon Formicidae resulted from the small number of toads in the sample. Campbell (1970) defined the utilization of Formicidae by toads within the perspective of a larger sample. Formicidae formed a stable portion of the diet.

The similarity of the diets of the frogs indicated that competition for food items may at times be acute as a result of a reduced abundance and availability of prey. However, the temporal separation between the ranids noted by Black (1969) and Dumas (1964) restricted the areas of competition. *Rana pretiosa* populated the mountain lakes, ponds, and streams; *Rana pipiens* inhabited the slough, ponds, and lake margins of the valleys. Both species coinhabited several locations in the foothill regions of the Flathead Valley.

The observed abundance of food items served to reduce potential competition between the ranids at coinhabited sites. The frogs were observed to remain segregated at coinhabited sites. At Mud Lake *Rana pretiosa* inhabited a relatively cold spring-fed stream while *Rana pipiens* inhabited the margin of the lake. At Roger's Lake, *Rana pretiosa* was seldom observed in the same locations as *Rana pipiens*. *Rana pretiosa* was common along the beach areas of the northern shore, and *Rana pipiens* was common along the vegetated margin of the southern shore of the lake.

Temporal separation also restricted potential competition between the ranids and the bufonid. The frogs were active diurnally and the toad was active nocturnally.

Conclusion

Rana pretiosa and *Rana pipiens* inhabited a variety of vegetated areas but avoided areas of extreme density and height. Both frogs remained close to the water.

The diets of the ranids exhibited similar taxonomic composition. However, dependence upon specific families of insects varied. The variations were attributed to differences in abundance and availability of item at the various sites. Ground-dwelling forms were predominant in the diets. As a result of the abundance of food items and temporal separation, competition between the ranids was reduced.

The diet of *Bufo boreas* consisted almost exclusively of ground-dwelling forms. Potential competition for food between the toad and the frogs was reduced by dietary and temporal separation.

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Literature Cited

Black, J. H. 1969. The frog genus *Rana* in Montana. Northw. Sci. 40:191-195.
————.1971. The toad genus *Bufo* in Montana. Northw. Sci. 45:156-162.
Campbell, J. 1970. Food habits of the boreal toad *Bufo boreas boreas* in the Colorado front range. Jour. of Herpetology. 14:83-85.
Dumas, P. C. 1964. Species-pair allopatry in the genera *Rana* and *Phrynosoma.* Ecology 45:178-181.
Kelby, J. D. 1945. A biological analysis of the food and feeding habits of two frogs, *Hyla c. cinera* and *R. p. sphenocephala.* Quart. Journal Fla. Acad. Sci. 8:71-104.
Linzey, D. W. 1967. Food of the leopard frog, *Rana p. pipiens,* in central New York. Herpetologica. 23:11-17.
Moore, J. E., and E. H. Strickland. 1954. Notes on the food of three species of Alberta amphibians. Amer. Midland Nat. 52:221-224.
————., and ————. 1956. Further notes on the food of Alberta amphibians. Amer. Midland Nat. 54:253-255.
Oliver, J. A. 1955. North American Amphibians and Reptiles. D. Van Nostrand Co., New York. 359 pp.
Turner, F. B. 1960. Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird & Girard, in Yellowstone Park, Wyoming. Ecological Mono. 30:251-278.
Whitaker, J. O., Jr. 1961. Habitat and food of mouse-trapped young *Rana pipiens* and *Rana clamitans.* Herpetologica. 17:173-279.

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Gravity Survey of the Cheney Quadrangle, Washington

Abstract

Gravity was measured at 247 stations in the area of the Cheney 15-minute quadrangle, eastern Washington, near the northern edge of the Columbia River Group basalt flows. Analysis of the data indicates: 1) A 20 mgal increase in the Bouguer anomaly from northwest to southeast; 2) A positive residual anomaly in the south-center of the map area suggesting an upthrown fault block of dense material in the basement; and 3) A possible northeast-trending fault in the basement rocks just north of the positive feature.

Because high residual gravity values are found associated with basement outcrops, the gravity data help delimit basement rocks and thus indicate the downward extent of permeable material, a potential aid in the search for groundwater. The method should be useful elsewhere along the margins of the basalts where interflow aquifers are important.

Introduction

The area of the gravity survey is represented by the Cheney 15-minute quadrangle, east-central Washington. This area, shown in Figure 1, comprises about 523 sq km (202 sq mi.). Figure 1 shows two small ruled areas which lie outside the Cheney quadrangle in the Sprague and Medical Lake quadrangles. Gravity measurements were made in the western ruled area because of the excellent elevation control available there. The ruled area to the north contains outcrops of rocks of the basement complex, and measurements were made there for comparison with the values obtained in the basaltic terrain of the Cheney quadrangle.

The oldest rocks in the Cheney quadrangle area are rocks of the pre-Tertiary crystalline basement complex and are exposed at the island in Bonnie Lake (SW¼ NE¼ Sec. 36, T.21N., R.41E.), where the rock is a massive fine- to medium-grained quartzofeldspathic gneiss; and at the northeast shore of Badger Lake (NE¼ SW¼ Sec. 34, T.22N., R.41E.), where the rock is a medium-grained quartzite with rust-colored spots and a few thin dark streaks of fine-grained biotite. The quartzite is very similar to that found at Fish Lake approximately 1.6 km north of the northeastern corner of the quadrangle. Griggs (1973) assigns a Precambrian age to the rocks at Fish Lake, classifying them in the Revett and Burke Formations, undivided, of the Belt Supergroup. Neither of the basement exposures in the Cheney quadrangle is indicated on Griggs' map. An additional basement exposure occurs approximately 1.6 km south of the study area between Bonnie Lake and Rock Lake.

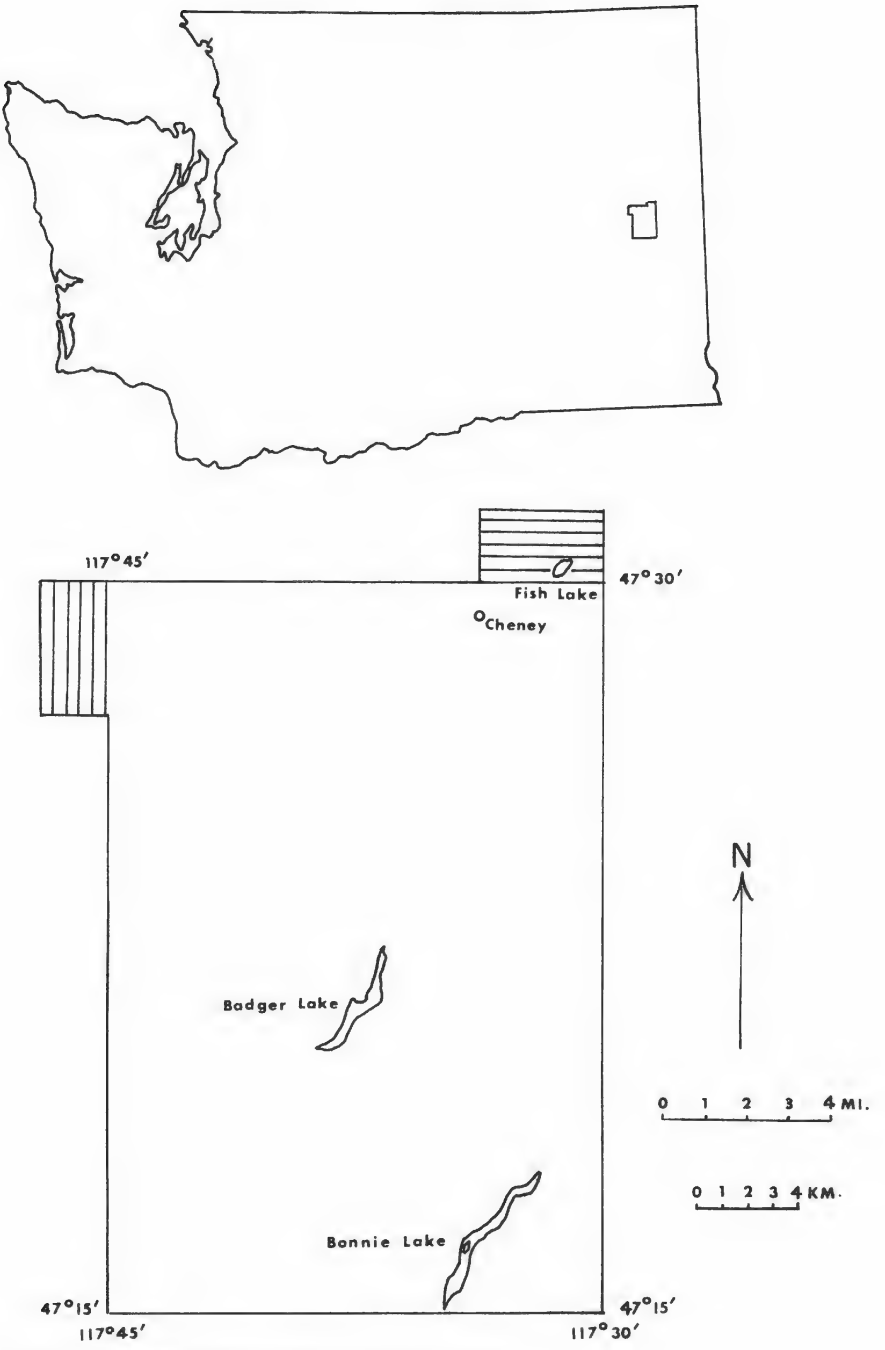


Figure 1. Index map showing location of the study area.

Basalt of the Columbia River Group covers much of the quadrangle; Swanson and others (1975) identify this rock as Yakima Basalt. The basalt consists of several flows which, locally, are nearly flat-lying (Newcomb, 1970). The flow tops are usually marked by thin rinds of vesicular or scoriaceous material that resulted from escaping gases while the lava cooled. Individual surface flows range in thickness from 8 to 37 m in the Cheney area (Olson and others, 1975, p. 13). East of the study area interbeds of the Latah Formation are intercalated between basalt flows. Thickness of the Latah is quite variable, ranging from exposures in excess of 30 m at Deep Creek near Spokane to a few centimeters in some wells near Cheney (Pardee and Bryan, 1926). No exposures of sedimentary interbeds have been seen in the Cheney quadrangle, but well logs indicate that they are present, at depth, in some places.

Two main types of unconsolidated material occur in the Cheney quadrangle: loess of the Palouse Formation and the gravels deposited during various periods of glaciofluvial activity in the Pleistocene Epoch. The Palouse loess is found at scattered locations within the quadrangle as are small deposits of glacial outwash gravels.

Previous gravity work within the Cheney quadrangle consists of the two stations shown on the Complete Bouguer Gravity Anomaly Map of Washington (Bonini and others, 1974). The state map lacks the density of stations in the Cheney area necessary to define the small features for which the present study was intended. A more recent Bouguer map of northeastern Washington and northern Idaho by Cady and Meyer (1976) shows one additional station in the Cheney quadrangle.

Field Work and Density Measurement

The gravity survey was conducted between September 14 and December 1, 1974. Preliminary work involved establishing a network of stations of known elevation. Of the bench marks indicated on the U.S.G.S. topographic map of the quadrangle, some are missing, buried, or have been moved. Those remaining were incorporated into the study as gravity stations. Because of the tight spacing of the planned survey grid (at least one station in each section of the Cheney quadrangle), elevation control was needed between bench marks and was established using an American Paulin System precision barometric altimeter graduated in two-foot increments. An accuracy of $\pm$ 3 feet was achieved by making short loops, usually less than two hours in duration, between bench marks. Additional control was attained by establishing stations at map locations having spot elevations which were then checked barometrically.

The gravity survey was conducted with a Worden geodetic gravimeter (instrument number 358). Of 247 measurements made, 245 were used in the survey. The other two were discarded as "wild values" unexplainably inconsistent with data from nearby stations. Average station spacing within the Cheney quadrangle is less than one mile.

The survey was tied to the national gravity base at Spokane International Airport. The gravity value at this station was taken from Report No. 144 of the Defense Mapping Agency Topographic Center (1974). A local base station was established at U.S.G.S. bench mark H263 at the Cheney Burlington Northern railroad station. All gravity survey loops began and ended there. Loops were usually closed two or three times a day, and meter drift corrections were computed for each loop. The drift correction also largely removes tidal effects. The estimated error due to meter reading inaccuracies is believed to be at most $\pm$ .05 mgal, and total error, including that due to elevation uncertainties, is estimated at less than $\pm$ .25 mgal at any station.

Collections of basement complex rocks, basalt specimens of various textures, and two samples of sedimentary rocks of the Latah Formation were made. Two methods were used to determine sample densities for most of the samples: a buoyancy method in which the sample was weighed in air and then immersed in water, and a method in which the mass and volume of a sample were determined separately. Table 1 summarizes the results of this work.

TABLE 1. Sample densities.

Sample Description	Location	Density (g/cm^3) Method 1*	Method 2*
Light quartzite	Fish Lake	2.64	2.65
Muscovite schist	Fish Lake	2.70	2.71
Fine-grained basalt	Badger Lake	2.85	2.87
Vesicular basalt	Badger Lake	2.59	—
Light quartzite	Badger Lake	2.53	2.58
Gray banded argillite	Granite Lake	—	2.68
Coarse-grained gneiss	Granite Lake	2.90	2.83
Quartzofeldspathic gneiss	Bonnie Lake	2.64	2.71
Mudstone (Latah Formation)	(?)	1.82	1.76
Basalt scoria	Depot Springs Road	1.76	—
Ultramafic dike (Prichard Formation)	Near Deer Lake, northern	2.76	2.81
Argillite (Prichard Formation)	Washington	2.69	2.64

*Method 1 is the buoyancy method; method 2 is the method whereby mass and volume are determined separately.

Data Reduction and Analysis

Values of gravity measured in the field were reduced for latitude, elevation, and local topographic effects. The principal facts for each gravity station (station number, latitude, longitude, elevation, observed gravity, theoretical gravity, simple Bouguer anomaly, terrain correction, and Bouguer anomaly including terrain correction) are available in concise tabular form from the authors. A standard station density of 2.67 gm/cm^3 was used in the elevation reduction. The reduced gravity data were contoured to produce a Bouguer anomaly map (Fig. 2). An additional Bouguer gravity map using data reduced with a density of 2.92 gm/cm^3 was prepared but was not included as the higher assumed density resulted in no meaningful change in interpretation. Corrections for local topographic effects were made using Hammer's (1939) tables and were carried out to zone J. In a majority of cases, the topographic effects were found to be negligible. A few stations, notably those on the shores of Bonnie Lake, Chapman Lake, and Williams Lake, required substantial corrections.

Polynomial trend surfaces of orders one through four were fitted by computer to the Bouguer anomaly data using the least squares criterion. The equations for the first and second order surfaces are

$$Z = -90.3383 + .4462X - .7705Y, \text{ and}$$

$$Z = -88.2571 + .4869X - 1.3572Y - .0158X^2 + 0.0138Y^2 + .0281XY,$$

where X is the distance in inches (original scale 1:62,500) from the west edge of the map, Y is the distance in inches measured northward from the south edge of the map, and Z is the Bouguer anomaly in mgal. As the coefficients of the second-degree terms are very small compared with the coefficients of the first-degree terms, the first order trend surface was used in the interpretation. This surface strikes N.59.9°E. and dips -.89 mgal/mile NW.

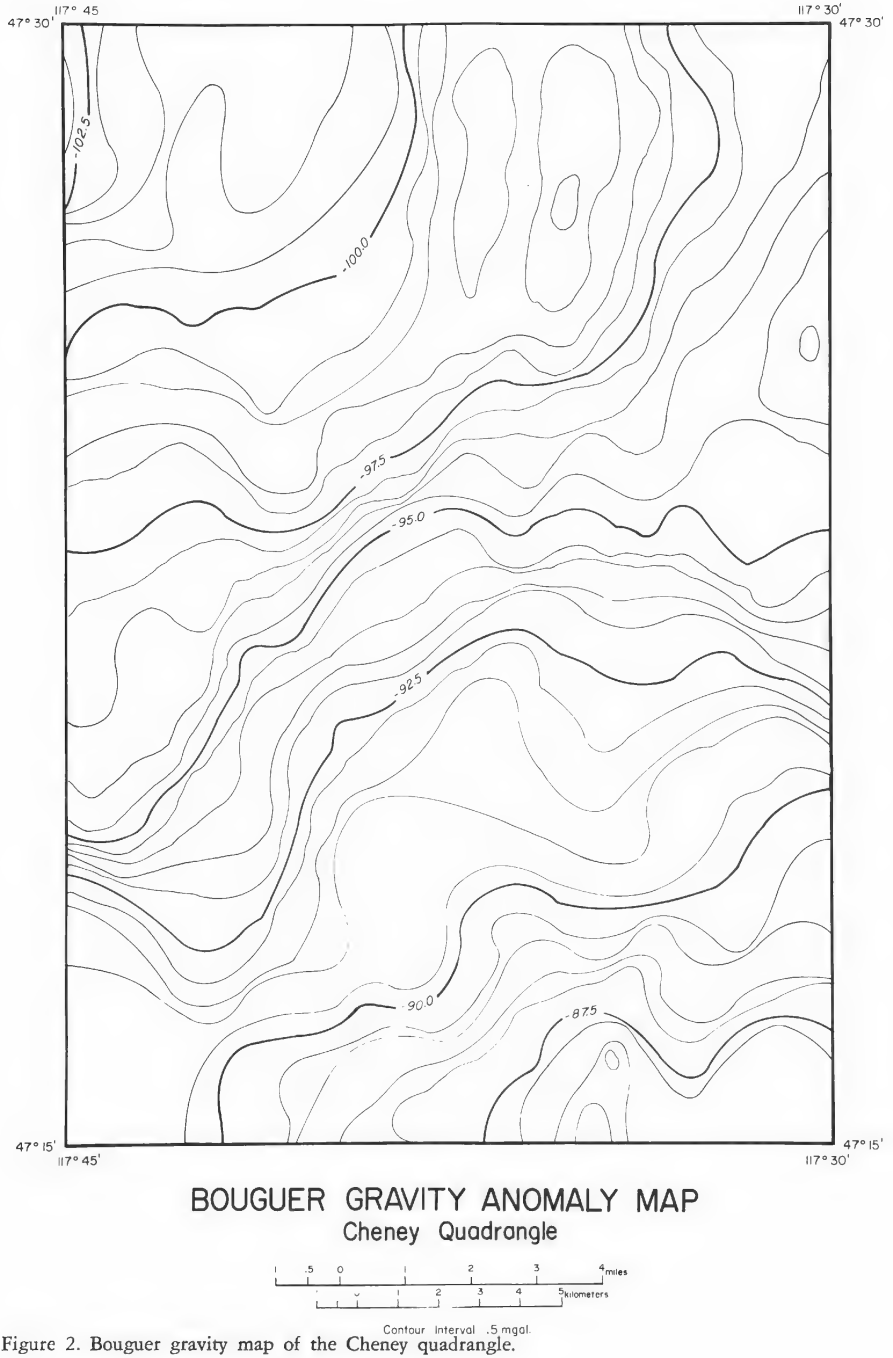


Figure 2. Bouguer gravity map of the Cheney quadrangle.

The computer was used to subtract the value predicted by the trend surface from the Bouguer anomaly value at each station, and the resulting residual values were hand-contoured to prepare the residual map (Fig. 3). Residual maps for four orders of trend surfaces were prepared by computer and were found to be very similar to the hand-contoured map but were somewhat over-smoothed as a result of the nature of the plotting routine.

The Gravity Anomalies

The Bouguer anomaly map (Fig. 2) shows a large negative anomaly throughout the study area. Maximum relief of this anomaly is approximately 20 mgal. The Bouguer gravity value is most negative in the northwestern corner of the area and becomes less negative toward the south. The maximum Bouguer gravity value was observed near the southeastern corner of the area. The Bouguer values on Figure 2 are not directly comparable with those reported by Bonini and others (1974) because the gravity value at the National Gravity Base Station at Spokane International Airport has been decreased by about 14 mgal recently (Defense Mapping Agency Topographic Center, 1974). A local steepening of the gradient from northwest to southeast is indicated near the center of the map. A similar, less well-defined gradient increase occurs in the southwestern corner of the map. These two features interrupt the otherwise gentle gradients in the map. The regional anomaly, defined as the first order trend surface, probably results from heterogeneity very deep in the crust.

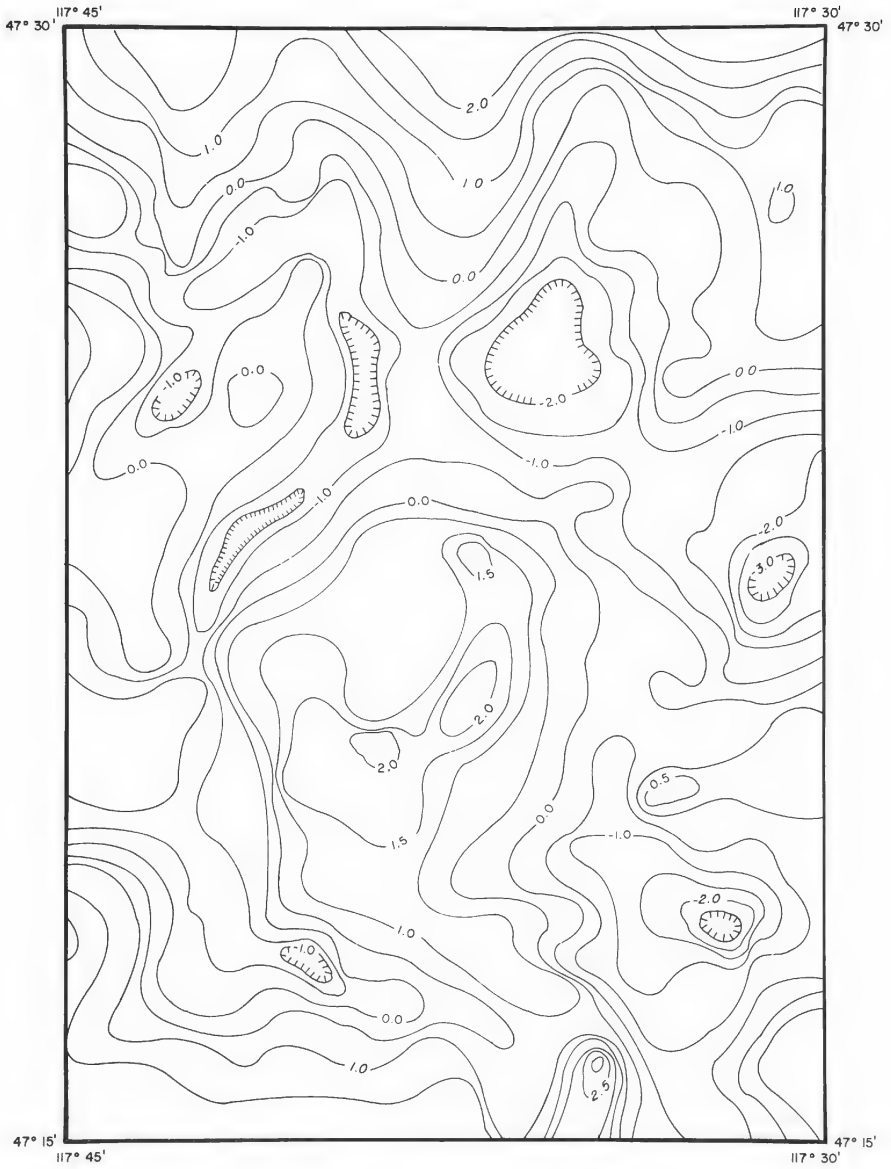
The residual map (Fig. 3), obtained by removing the planar regional anomaly from the Bouguer map, shows positive residuals along the northern and the southern borders and in the south-central part of the survey area. Negative anomalies appear on the eastern edge and in the north-central part of the area. The steepening of the gradient which occurs near the center of the Bouguer map (Fig. 2) is expressed as a series of strong negative anomalies trending NE-SW on the residual map (Fig. 3). A broad positive anomaly in the south-central part of the residual map corresponds to the gently sloping surface in the south part of the Bouguer map. This broad positive anomaly reaches its maximum value just south of the center of the map in the vicinity of Badger Lake. The strongest positive residual anomaly occurs just east of the center of the southern border of the map at Bonnie Lake.

Interpretation

No unique interpretation of the subsurface geology is possible based on the gravity data alone. However, a comparison of the major anomalies with the gravity effects calculated for various simple geometric forms provides a reasonable and self-consistent explanation (illustrated in Fig. 4) of the regional anomaly map as follows:

1. An unexpected characteristic of the residual anomaly, and probably the most significant result for groundwater prospecting, is that positive anomalies are located in areas where rocks of the basement complex are exposed. This relationship is seen at the three areas where basement rocks outcrop: at Fish Lake, just north of the survey area; at Bonnie Lake; and near Badger Lake. The relationship between this result and expected density contrasts is discussed in the next section.

2. The northeast-trending series of gravity lows just north of the center of the residual map may be the signature of a valley in the basement rocks partially filled with sedimentary material pre-dating the blanket of Yakima Basalt now covering the area. Such a valley may follow a fault in the older rocks.



RESIDUAL ANOMALY MAP

Cheney Quadrangle

1 .5 0 1 2 3 4 miles

1 .5 0 1 2 3 4 5 kilometers

Contour interval 0.5 mgal

Figure 3. Residual Bouguer gravity map.

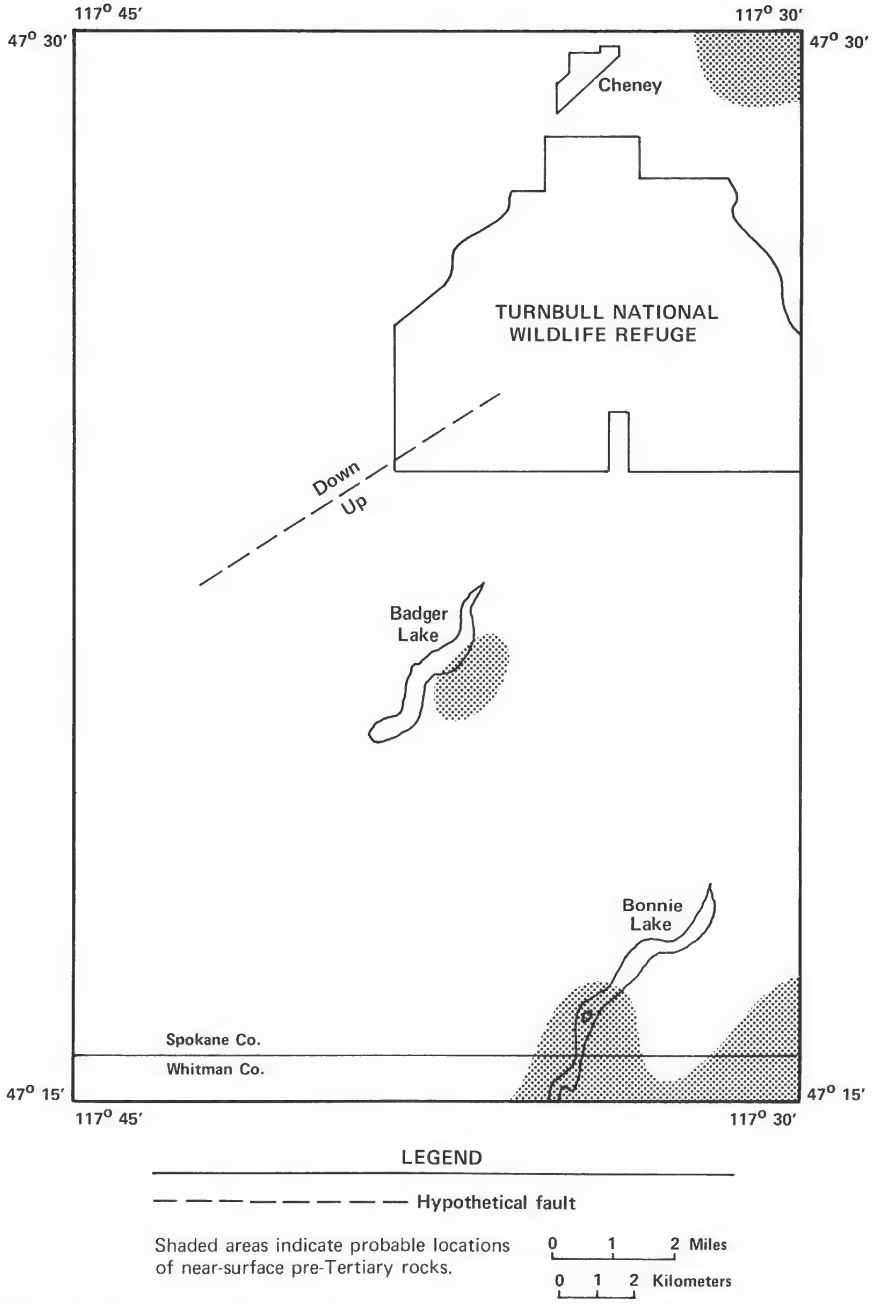


Figure 4. Interpretation of gravity data.

3. The broad positive anomaly in the south center of the map area may be the expression of a deep-seated intrusive body or a buried ridge of dense pre-Tertiary material. The anomaly may also indicate the presence of a fault block underlain by dense material at depth. The latter hypothesis is preferred because the linear negative feature to the north appears to represent a fault, and because the large positive anomalies at Fish Lake and Bonnie Lake in basement rocks appear to confirm the existence of denser material below the surface in basement rocks. If the quartzite exposed at Fish Lake belongs to the Burke Formation, the denser material may correspond to the underlying Prichard Formation, which is known to contain extensive mafic intrusive bodies elsewhere in eastern Washington (Griggs, 1973). Trial and error calculations in which the source of the anomaly is treated as a horizontal slab indicate a thickness of 120 m assuming a density contrast of .2 gm/cm^3.

4. A northwest-trending fracture zone mapped by Griggs (1973) in the southwest part of the area shows no gravity signature, perhaps because the zone is confined to near-surface rocks.

5. The gravity maps show no trends parallel to the much-discussed Olympic-Wallowa-Lineament first described by Raisz (1945).

Relationship to Measured Densities

The calculations mentioned in the preceding section comparing the gravitational effects of simple geometric forms to the observed anomalies indicate that the sources of the anomalies lie below the basalt-basement interface and that no large density contrast exists between the Tertiary rock column, including the basalts, and the upper basement. The fact that the outcrops of basement invariably have associated positive anomalies implies that the aggregate density of the Tertiary column is less than that of the basement complex. This result can be explained by examining the nature of the Tertiary column.

Table 1 indicates that the densities of the pre-Tertiary metamorphic rocks collected in the study area do not differ much from a mean value of 2.65 g/cm^3 with the exception of the gneiss from Granite Lake north of the study area. In order to justify the conclusion that the density contrast between the Tertiary column and the upper basement is small, the rocks of the Tertiary column must also exhibit an aggregate density of about 2.65 g/cm^3.

The average density of massive basalt from the Cheney area is 2.86 g/cm^3. Vesicular basalt has a density of 2.59 g/cm^3, and basalt scoria averages 2.05 g/cm^3. The last figure is a bit high since no attempt was made to isolate the air pockets in the surface of the samples during the density determinations. The Latah Formation is Tertiary in age and occurs as sedimentary layers at the base of, and interbedded with, the basalt flows of the Columbia River Group in the Spokane area. The density of this material is about 2.0 g/cm^3.

Basalt flows of the Columbia River Group are characterized by their great lateral extent and by the striking similarity of the flows over wide areas. Lefebvre (1970, p. 34-35) has tabulated various physical characteristics of 22 such flows in the Grand Coulee area. It seems reasonable to infer that some of these characteristics may be extended to basalt flows in the Cheney area. Thirty-five percent of the total thickness of the basalt flows tabulated by Lefebvre is described as vesicular. If 5 percent of the basalt

is assumed to be scoriaceous and 60 percent to be massive, then the aggregate density of the basalt is 2.72 g/cm^3. Then, if 10 percent of the Tertiary rock column is sedimentary and 90 percent is basalt, a density of 2.65 g/cm^3 is obtained as an average.

The percentages of various materials cited above are quite reasonable. The average thickness of sediments calculated from twenty-five water well logs from the study area (obtained from the Washington Department of Ecology office, Spokane) averages 9 percent of the total depth of the wells. Many of the wells used are shallow (less than 60 m), but thicker sedimentary beds are known to occur at depths of 120 m or more (Olson and others, 1975). At the time of writing, the City of Cheney is drilling an exploratory water well immediately west of town and appears to have struck basement 352 m below the surface after having penetrated 64 m of lake sediments in two different horizons (Salter, pers. comm.). Figure 3 indicates a residual anomaly of 0.5 mgal at the location of the well.

The variable thickness of the low density sedimentary interbeds and the presence of variable density rocks in the basement complex make an exact quantitative estimation of basalt thickness impossible. On a large scale, pre-Tertiary rocks are not necessarily associated with high gravity values as can be seen by comparing the map of Cady and Meyer (1976) with the geologic map of Griggs (1973), and the whole problem of density contrast is far more complex.

Application to Groundwater Discovery

Groundwater in the Cheney area comes primarily from basalt aquifers. This study shows that positive residual anomalies are associated with exposures of the pre-Tertiary basement complex, rocks which because of their impermeability are poor producers of groundwater. Thus, in areas showing positive residual anomalies, water would be expected to occur at shallow depths if at all. In areas with negative residuals, the basement rocks would be expected to lie at depth, and water should occur in relative abundance in the intervening Tertiary rock column.

Conclusions

Explanation of the survey results required the development of a new way of interpreting the gravity effects of the Tertiary rock column, viz., that the average density of the column is significantly lower than the density of massive basalt. Evidence was found for a northeast-trending fault or a valley in the basement complex. The association of positive residual anomalies with outcrops of basement rocks should prove helpful for locating groundwater in the Cheney area, and the method may also apply in other areas near the margin of the Columbia Plateau.

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Literature Cited

Anonymous. 1942. Theoretical Gravity at Sea Level for Each Minute of Latitude by the International Formula: Washington, D.C., U.S. Dept. of Commerce, Coast and Geodetic Survey. 10 pp.

Bonini, W. E., D. W. Hughes, and Z. F. Daneš. 1974. Complete Bouguer gravity anomaly map of Washington: Washington Div. Geology and Earth Resources Geologic Map GM-11.

Cady, J. W., and R. F. Meyer. 1976. Bouguer gravity map of the Okanogan, Sandpoint, Ritzville, and Spokane 1° x 2° quadrangles, northeastern Washington and northern Idaho: U.S. Geol. Survey Geophys. Inv. Map GP-914.

Davis, J. C. 1973. Statistics and Data Analysis in Geology. John Wiley and Sons, New York. 550 pp.
Defense Mapping Agency Topographic Center. 1974. Combined Oregon and Washington state base nets: Dept. of Geodesy Report No. 144, September 9, 1974.
Griggs, A. B. 1973. Geologic map of the Spokane quadrangle, Washington, Idaho, and Montana: U.S. Geol. Survey Misc. Geol. Inv. Map I-768.
Hammer, S. 1939. Terrain corrections for gravimeter stations: Geophysics. 4:184-194.
Lefebvre, R. H. 1970. Columbia River Basalts of the Grand Coulee area, pp. 1-39 *in* Proceedings of the Second Annual Columbia River Basalt Symposium. Eastern Washington State College Press, Cheney. 333 pp.
Newcomb, R. C. 1970. Tectonic structure of the main part of the basalt of the Columbia River Group, Washington, Oregon, and Idaho. U.S. Geol. Survey Misc. Geol. Inv. Map I-587.
Olson, T. M., E. H. Gilmour, M. Bacon, J. L. Gaddy, G. A. Robinson, and O. J. Parker. 1975. Geology, Groundwater, and Water Quality of Part of Southern Spokane County, Washington—Project completion report U.S. Dept. of Interior, Office of Water Resources and Research. 139 pp.
Pardee, J. T., and K. Bryan. 1926. Geology of the Latah Formation in relation to the lavas of the Columbia Plateau near Spokane, Washington: U.S. Geol. Survey Prof. Paper 140-A, pp. 1-16.
Raisz, E. 1945. The Olympic-Wallowa Lineament: Am. J. Sci. 243-A: 479-485.
Salter, A. Personal communication, Street Department, Cheney, Washington.
Swanson, D. A., T. L. Wright, and R. T. Helz. 1975. Linear vent systems and estimated rates of magma production and eruption for the Yakima Basalt on the Columbia Plateau: Am. J. Sci. 275:877-905.

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Osprey Distribution, Abundance, and Status in Western North America: I. The Northern California Population

Abstract

An estimated 355± 40 pairs (95 percent C.I.) of Ospreys (*Pandion haliaetus carolinensis*) nested in the northern California survey area in 1975. Eighty-one pairs were estimated along the extreme northern coast in Del Norte and Humboldt Counties. One hundred and forty-four pairs were estimated along California's northern coast in Mendocino, Sonoma, and Marin Counties. The northern interior region, primarily in Siskiyou, Trinity, Shasta, Lassen, and Plumas Counties, contained an estimated 130 pairs. Forty-nine percent of the interior Osprey population is associated with reservoirs that were not present in 1900. We believe more Ospreys are present in the interior now than 75 years ago because of the increase in suitable habitat; nevertheless, populations at Shasta Lake and Clair Engle Lake are now exhibiting below-normal production rates and local declines. The long-term status of the coastal population, nesting along rivers, streams, and bays, is not clear. Recent production rates from two segments of the coastal population appear to be normal, but production at Usal Creek is below normal.

Introduction

Ospreys received little attention in North America until Ames and Mersereau (1964) and Ames (1966) documented the population crash of the Connecticut River colony in the northeastern United States and implicated pesticides as the primary cause for its decline. Amazingly, since 1964, at least parts of most Osprey populations throughout North America, including the California populations, have been studied (see review by Henny, 1977). Historical information about the California population is sparse and much of it is descriptive, lacking quantitative treatment. Grinnell (1915) discussed

three general regions of California where breeding Ospreys occurred: (1) the northern coastal population, (2) the northern interior population, and (3) the Channel Islands and central and southern coastal population. The Channel Island population disappeared between 1917 and 1968 (Diamond, 1969; Lynch and Johnson, 1974). Kiff (pers. comm.) reported no records of Ospreys breeding on any of the Channel Islands after 1927, although there were later (1939) sightings during the breeding season. Diamond (1969:60) further noted that the species declined virtually to extinction on the mainland of central and southern California during the same period of time. However, two nesting records were reported in southern California in 1975; one at Tinnemaha Reservoir, Inyo County, and another at San Antonio Lake, Santa Barbara County (American Birds, 1975). Therefore, we believe that large nesting populations are generally restricted to the northern coastal and northern interior parts of California.

Although segments of rivers and parts of lakes and reservoirs in California have been studied intensively, no rigorous survey of Osprey habitat in the northern part of the state has been made. Information on the present distribution and abundance of Ospreys in this region is needed to locate concentration centers and other nesting locations which may be in immediate danger from disturbance, and to obtain information for evaluating future changes in distribution and abundance. Furthermore, this report attempts to synthesize available information on the status of the species in California.

The present distribution and abundance of Ospreys is based on an aerial survey procedure developed and tested in Chesapeake Bay in 1973 (Henny *et al.*, 1974). The survey involves an aerial count and a nearly simultaneous ground count made over a part of the area surveyed from the air. This comparison made possible the development of an aerial visibility rate that was used to adjust aerial counts to the total number of occupied nests, including those not seen from the air. This approach works well for Ospreys in northern California because: (1) the nest sites are conspicuous, (2) the nesting habitat is limited, and (3) the nesting cycle is highly synchronized. The same procedure has been used along the Atlantic Coast to estimate the size of Osprey populations in New Jersey, Delaware, Maryland, Virginia, North Carolina, and South Carolina (Henny and Noltemeier, 1975; Henny *et al.*, 1977). Supplementary information concerning productivity was used in previous studies and will be used again here to evaluate the condition of the nesting populations.

Methods and Materials

Occupied Osprey nests were located by flying a Cessna 206 aircraft about 60 m above the ground along the coastline, rivers, lakes, and reservoirs of northern California. The upper segments of most rivers were not surveyed because the amount of water there was believed insufficient to maintain nesting Ospreys. However, Ospreys are occasionally found nesting in areas where they are least suspected, sometimes at considerable distances from water. Boundaries for this survey are shown in Figure 1; the lakes and reservoirs surveyed are given in the Appendix. Several pairs nested outside the survey boundaries (one pair at the Truckee River, another at Lake Tahoe), but time did not permit a survey of all Osprey habitat in the northern part of the state. Likewise, Jewett (1923) reported four Osprey nesting records in the rolling, rocky, arid desert land of Modoc County in 1922. Modoc County was not surveyed in 1975. The total population estimate only reflects the area surveyed (possibly 90-95 percent of suitable Osprey habi-

tat); therefore, the estimate is low for the northern California population.

The aerial survey took about 60 hours of flying time. We located nests from the air between 14 and 21 May 1975. Ground counts were made almost simultaneously at selected locations by boat, on foot, or in a pickup truck. A nest was considered to be occupied if an Osprey was at or near the nest site when the survey was made, and nearly all of the occupied nests had adults incubating eggs. The air:ground comparison procedure provides an assessment of the consistency and reliability of the aerial counts, in

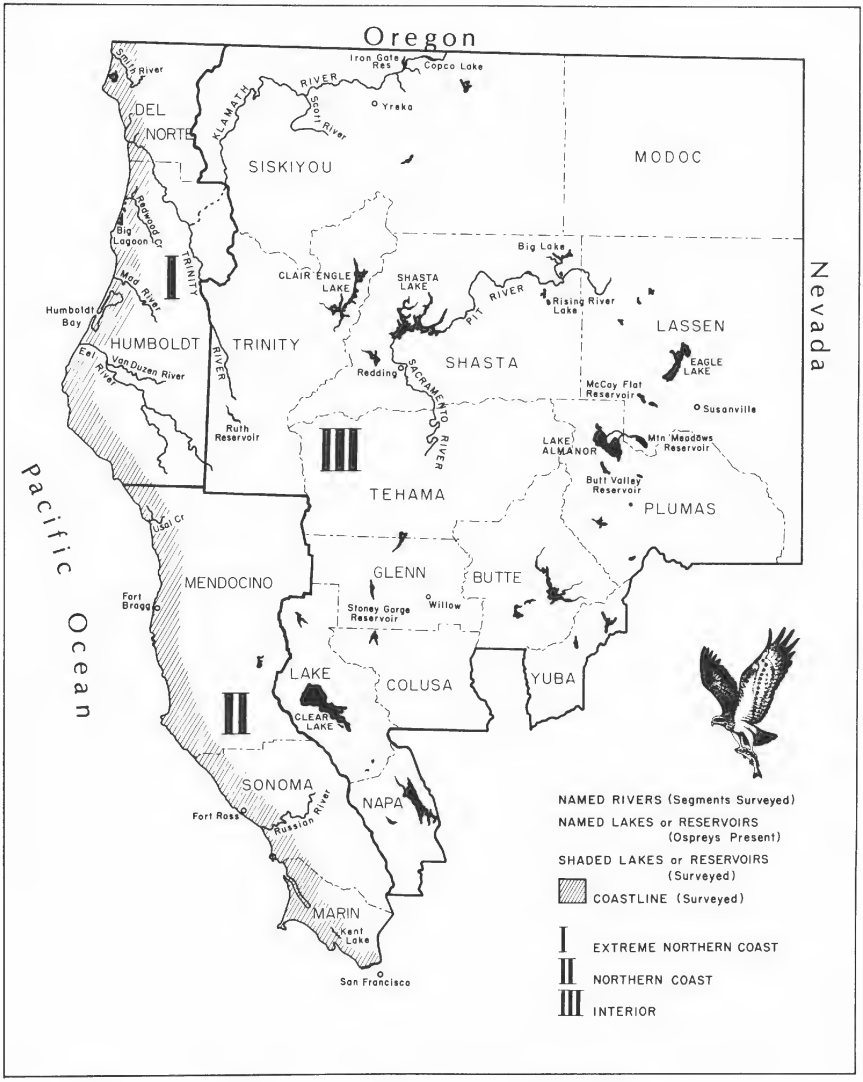

Figure 1. The northern California survey area in 1975.

addition to providing adjustments for occupied nests missed during the aerial survey.

The procedure for estimating the total nesting population and its associated visibility rate is a modification of the Petersen Estimator method and is a double sampling technique (Henny *et al.*, 1974; Henny and Noltemeier, 1975). We let a finite population of size N (N unknown) be sampled by two methods. The data are then recorded so that we know n_1, the number of elements observed by method 1 (aerial survey); n_2, the number of elements observed by method 2 (ground survey); and m, the number of identical elements observed by both methods. Then,

$$\hat{N} = \frac{n_1 n_2}{m}$$

is a reasonably good estimator of N (the total nesting population in a given area). Thus $\hat{N}/n_1$ becomes the estimator of the aerial visibility rate. The initial approach for calculating the variance (Henny *et al.*, 1974) yielded an estimate that was biased slightly low. In the present paper, an improved procedure discussed by Henny and Noltemeier (1975) was followed.

Aerial counts in locations not surveyed from the ground were adjusted by the aerial visibility rates obtained at similar habitats. Nearly all of the Osprey habitat in northern California was surveyed from the air, but only a selected part was surveyed from the ground because of the time required for ground surveys.

The occupied nests along rivers in northern California were difficult to locate from the air because many of the streams flowed through deep canyons which prevented low-level flights. Failure to observe such nests results in a higher adjustment factor since more nests were presumed missed. Therefore, since nearly all nests were in live or dead trees, visibility rate estimates were classified according to the types of habitat in which the nests were located (rivers vs. lakes and reservoirs), rather than according to the types of nest sites (i.e., trees, duck blinds, channel markers, etc.). The one exception to this procedure was the nesting platforms at Eagle Lake which were extremely visible from the air and a separate visibility rate was calculated for them. The visibility rates in Table 1 appear reasonable; nesting platforms at Eagle Lake were the most visible (1.18),

TABLE 1. Number of occupied Osprey nests (nesting pairs) seen from the air and the ground.

Nest Site Types	Air n_1	Ground n_2	Both m	Total est. $\hat{N}$	Visibility rate $\hat{N}/n_1$
Nesting platforms[a]	11	13	11	13.00	1.18
Trees (lakes-reservoirs)[b]	41	54	31	71.42	1.74
Trees (rivers)	31	57	20	88.35	2.85

[a]Short platforms at Eagle Lake.
[b]Includes a few nests on power poles or towers and several platforms placed on the tops of live trees at Lake Almanor.

tree nests around the lakes and reservoirs were moderately visible (1.74), and tree nests along the rivers were least visible (2.85). The visibility of tree nests around lakes and reservoirs was nearly the same as the visibility of tree nests around the bays and sounds of North and South Carolina (visibility rate = 1.70; Henny and Noltemeier, 1975). Occupied nests within the area surveyed, but missed by both aerial and ground surveys, are accounted for in our estimates. The estimated numbers of nesting pairs may include a few nonbreeding birds (Henny and VanVelzen, 1972).

Results

Distribution and Abundance

The distribution and abundance of nesting Ospreys are discussed in terms of three geographical regions for the area north of San Francisco in northern California: (1) the extreme northern coastal region (Del Norte and Humboldt Counties), (2) the northern coastal region (Mendocino, Sonoma, and Marin Counties), and (3) the northern interior region. The study area was subdivided because the coastal populations were associated primarily with the coastal streams and Humboldt Bay, whereas the interior populations were concentrated primarily around lakes and reservoirs except for Osprey nesting on the Klamath River.

Each region was further subdivided into several segments. These segments were composed of lakes, reservoirs, rivers, or groups of lakes, reservoirs, or rivers. The estimated total numbers of pairs in each segment within each region is generally reliable, but the combined estimate of all segments within each region as a whole is more reliable. Segments with large differences between the maximum number of pairs observed and the total estimate are the least reliable.

Extreme Northern Coastal Population (Region I). An estimated 81 pairs of Ospreys nested in Del Norte and Humboldt Counties in 1975; these were concentrated in the timber above Humboldt Bay (35 pairs), along the Eel River and its tributaries (23 pairs), and along the Klamath and Trinity Rivers (11 pairs). The remainder was scattered throughout the two counties (Table 2). In an incomplete survey in the early

TABLE 2. The distribution of occupied Osprey nests (nesting pairs) in coastal northern California (area above San Francisco) in 1975.

Location		Nesting Pairs Max. obs.[a]	Total estimate
Extreme Northern Coastal Population (Del Norte-Humboldt Counties)			
Klamath River and Trinity River		7	(11.40)[b]
Humboldt Bay and vicinity		20	(34.80)[c]
Eel River and tributaries		12	(23.05)[d]
Remainder[e]		4	(11.40)[b]
	Subtotal	43	81
Northern Coastal Population (Mendocino-Sonoma-Marin Counties)			
Usal Creek		23	(28.50)[b]
Ft. Bragg-Ft. Ross		30	(85.50)[b]
Russian River and tributaries		15	(22.80)[b]
Kent Lake		7	(7.00)[f]
	Subtotal	75	144
	Total	118	225

[a]Maximum number observed (located from air and/or ground).
[b]Aerial visibility rate of 2.85 X air count.
[c]Aerial visibility rate of 1.74 X air count.
[d]Aerial visibility rate of 2.85 X air count, plus 3.10 nests in area not surveyed by air (2 observed from ground X ground visibility rate of 1.55).
[e]Includes sightings from air on Smith River (1), Redwood Creek (1), Mad River (1), and Big Lagoon (1).
[f]Total count of small lake.

1970s, French (1972) found 49 pairs nesting in Humboldt and Del Norte Counties—18 pairs above Humboldt Bay, 13 pairs along the Eel River and its tributaries, 12 pairs along the Klamath and Trinity Rivers, and the remainder scattered elsewhere in the

two counties. Ueoka and Koplin (1973) have studied the foraging behavior of the population that fishes in south Humboldt Bay.

Northern Coastal Population (Region II). The estimated 144 pairs of Ospreys within this three-county area were concentrated along the larger rivers and small streams (Table 2). The Usal Creek drainage in northern Mendocino County was the nesting location for an estimated 29 pairs. The small coastal streams between Ft. Bragg and Ft. Ross, a distance of approximately 120 km, provided nest sites for another 86 pairs. The remaining pairs were concentrated along the Russian River and its tributaries and at Kent Lake. French (1972) found 14 pairs in the Usal Creek drainage during a ground survey in 1971.

Northern Interior Population (Region III). An estimated 130 pairs of Ospreys nested in the interior part of northern California in 1975 (Table 3). An estimated 72 percent

TABLE 3. The distribution of occupied Osprey nests (nesting pairs) in the interior of northern California in 1975.

Location	Nesting Pairs	
	Max. obs.[a]	Total estimate
Northern Interior Population		
Klamath River [b]	15	(19.95)[c]
Scott River	5	(7.75)[d]
Clair Engle Lake	5	(5.22)[e]
Shasta Lake	20	(20.00)[f]
Eagle Lake (short platforms)	13	(13.00)[g]
(other sites)	9	(10.44)[e]
Lake Almanor	16	(15.66)[e]
McCoy Flat Res. + Mtn. Meadow Res. + Butt Valley Res.	9	(8.70)[e]
Big Lake + Rising River Lake (including Fall River)	14	(18.40)[h]
Remainder (lakes or reservoirs)	3	(5.22)[e]
Remainder (rivers)	2	(5.70)[c]
Total	111	130

[a]Maximum number observed (located from air and/or ground).
[b]Includes Iron Gate Reservoir and Copco Lake on Klamath River.
[c]Aerial visibility rate of 2.85 X air count.
[d]Ground count only; ground count X 1.55.
[e]Aerial visibility rate of 1.74 X air count.
[f]Believed to be total count.
[g]Aerial visibility rate of 1.18 X air count.
[h]Aerial visibility rate of 2.30 X air count, as about half of birds near lakes and remainder near river. This area surveyed in 1976.

of this total nested on lakes or reservoirs, mainly at Eagle Lake, Shasta Lake, Lake Almanor, Big Lake, and Clair Engle Lake. The remaining 28 percent nested along rivers, the most important being the Klamath River (parts of which were included in Region I), which includes Iron Gate Reservoir and Copco Lake, and its tributary, the Scott River.

One pair each of nesting Ospreys were also found at Clear Lake, Stony Gorge Reservoir, Ruth Reservoir, south fork of Trinity River, and on the Sacramento River near Anderson. Since other pairs undoubtedly were present in the region, adjustments in the total estimate were made accordingly. Herman (pers. comm.) recorded one pair of Ospreys fledging two young at Clear Lake in 1966.

Nesting Locations

Nest Sites. An estimated 92 percent of all Ospreys nesting in northern California were found in trees (primarily dead snags or trees with dead tops), 5 percent on man-made Osprey nesting platforms, 2 percent on power transmission poles or towers, and the remainder on miscellaneous structures including a National Forest observation tower (Table 4).

TABLE 4. Nesting sites utilized by Ospreys in northern California in 1975.

	Location			
Category	Region I	Region II	Region III	Total
Nests in trees[a]	100%	100%	79%	92%
Nests along man-made reservoirs	0%	5%	49%	20%
Estimated total number nesting pairs	81	144	130	355

[a]Unaltered trees. Excludes trees with platforms constructed on top at Lake Almanor.

Nest sites vary regionally. All nests along the northern coast were in trees whereas only 79 percent of nests in the interior region were in trees. Part of the 21 percent that were not in trees were built on platforms provided by the U.S. Forest Service for Ospreys at Eagle Lake and Lake Almanor. However, power poles or towers, associated with hydroelectric power plants, were also of some importance to nesting pairs in the interior.

Nest Site Surroundings. How important are man-made reservoirs to nesting Ospreys in California? Studies along the Atlantic Coast show that the species is adaptable and responds to favorable habitat change (Henny and Noltemeier, 1975).

An estimated 20 percent of the pairs of Ospreys in northern California in 1975 nested along reservoirs, habitat that was not available 75 years ago (Table 4). Of particular note is the importance of reservoirs to the interior population; nearly half (49 percent) utilize man-made lakes. Because fewer reservoirs are present in the coastal region, only a limited number of Ospreys are utilizing them. Reservoirs important to nesting Ospreys in northern California and the year they were completed, as reported by Martin and Hanson (1966), are, in order of importance: Shasta Lake (1949), Lake Almanor (1913), Kent Lake (1954), Clair Engle Lake (1960), Butt Valley Reservoir (1924), Copco Lake (1917), Iron Gate Reservoir (1963), McCoy Flat Reservoir (1891), Mountain Meadows Reservoir (1924), Clear Lake (1915), Stony Gorge Reservoir (1928), and Ruth Reservoir (1962).

Status of the Population

Two general methods of assessing the status of Osprey populations are available: (1) a comparison of observed production rates with a standard necessary for maintaining a stable population, and (2) a comparison of present populations with historical information for given locations. Henny and Wight (1969) provided a production standard for Ospreys based on data from eastern North America. They estimated that 0.95 to 1.30 young must fledge annually per breeding pair to maintain a stable population. The standard was reviewed recently by Henny (1977), with respect to numerous published studies, and was found to be reliable. However, Henny cautioned that observed production rates obtained from short-term studies or small localized study areas should be in-

terpreted with caution. Likewise, a comparison of the number of pairs nesting over a period of time on relatively small study areas must be interpreted with caution, inasmuch as Ospreys will pioneer newly-created nesting habitat such as the reservoirs mentioned above.

Production Standard. Several segments of the northern California Osprey population have been studied intensively and their production rates have been reported (Table 5).

TABLE 5. Observed Osprey productivity in northern California.

Location	Year(s)	Number of occupied nests	Percent nests successful[a]	Fledglings/ occupied nest	Authority
Lassen and Plumas Co.[b]	1969-71	136	54	1.02	Kahl (1971), Garber (1972)
Klamath Natl. Forest	1969-74	87	61	1.03	Gale and Forbis (1974)
North Coast	1971-72	49	65	1.19	French (1972)
Usal Creek	1971	14	43	0.50	French (1972)
Shasta Lake	1969-71	59	-	0.83	Gordon (pers. comm.)
	1972-75	72	-	0.81	Gordon (pers. comm.)
Clair Engle Lake	1972-75	20	-	0.50	Gordon (pers. comm.)

[a]Fledged at least one young.
[b]Includes Eagle Lake, Lake Almanor, and adjacent reservoirs, lakes and rivers.

If we assume that Henny and Wight's (1969) production standard based on data from the East is applicable to western populations, the production rates are within the normal range except at Usal Creek, Shasta Lake, and Clair Engle Lake.

Present vs. Historical Populations. Much of the intensive survey effort in recent years has been focused on the interior population. To our knowledge, no historical quantitative data are available on the northern coastal population. The best historical records of Ospreys in northern California are from Eagle Lake, one of the few natural lakes in the region. Eagle Lake is probably the primary source for the pioneering birds that colonized the reservoirs in the interior. The numbers of breeding pairs observed at the lake for the period 1905-75 are shown in Table 6. The low numbers in the early years (1905

TABLE 6. History of Osprey nesting records at Eagle Lake.

Year	No. nesting pairs	Authority
1905	2	Sheldon (1907)
1914	6+	Ray (1915)
1921	30-35	Grinnell et al. (1930)
1925	30-35+	Grinnell et al. (1930)
1969	18	Kahl (1971)
1970	24	Garber (1972)
1971	24	Garber (1972)
1975	23	Present study

and 1914) were probably based on incomplete counts; we know the 1914 count was incomplete from the text of the report. The counts for 1921 and 1925 were reported as estimates of the complete breeding population. Kahl (1971) believed that the apparent increase in Ospreys at Eagle Lake from 1905 to 1925 probably was related to the large numbers of snags produced when trees were killed as the lake level rose naturally about 12 feet from 1880 until 1915. The rising lake submerged and drowned trees over an extensive area around the south and west shorelines. This area later was exposed when the

lake level dropped in 1917. The snags offered ideal nesting habitat for Ospreys. Since the shoreline flooding of Eagle Lake over 60 years ago, the disintegrating forces of nature, aided by man, have reduced considerably the numbers of standing snags. Kahl (1971) believed the reduction in numbers of Ospreys at Eagle Lake probably was associated with the decline in nesting snags. We concur, and further believe that the shortage of nest sites at Eagle Lake forced the progeny to look for other locations at about the time reservoirs were being constructed throughout the interior of northern California (see construction dates mentioned earlier). The counts of nesting pairs have ranged from 18 to 24 between 1969 and 1975. Probably there are currently more Ospreys at Eagle Lake than between 1900 and 1915, but fewer than between 1915 and 1925.

Some information is available on recent numbers at Lake Almanor, Shasta Lake, and Clair Engle Lake which are all reservoirs. Fourteen pairs were reported at Lake Almanor in 1969 (Kahl 1971), and 16 pairs in both 1970 and 1971 (Garber 1972). We also saw 16 pairs at Lake Almanor in 1975 (Table 3). Excluding the first year of study in the Shasta-Trinity National Forest, when surveys were probably less complete, the numbers of nesting Ospreys at Shasta Lake and Clair Engle Lake are declining: 1970 (30 pairs), 1971 (25), 1972 (25), 1973 (23), 1974 (21), and 1975 (23). The ground count information was provided by James Gordon (pers. comm.). We documented 25 pairs at the two lakes in 1975 (Table 3) with our aerial survey and ground counts, but, to keep the series of data comparable, we mention only the ground count information above.

Discussion and Recommendations

This study was designed to provide information on the distribution and abundance of Ospreys in northern California in 1975, and to evaluate the status of geographical segments of the population. An estimated 355 ± 40 pairs nested in northern California in 1975, 63 percent along the coast and 37 percent in the interior. The coastal population is the more typical of the two in that it nests solely in trees along rivers, streams, bays, and at one man-made reservoir (Kent Lake in Marin County). The interior population is less typical and nests near reservoirs and on man-made structures (nesting platforms, power poles) instead of in trees. These artificial substrates are becoming more important as nesting sites in the interior.

Recent productivity at Eagle Lake and other locations in Lassen and Plumas Counties appears to be normal and no changes in Osprey numbers are apparent. In contrast, productivity at Shasta Lake and Clair Engle Lake appears to be below normal and the populations have declined in recent years. We recommend: (1) further study in the Shasta-Trinity National Forest to identify factors responsible for the low productivity and population decline (human disturbance and pesticides are two factors to evaluate); (2) continued monitoring of populations in the National Forests and on other public lands; and (3) initiating Osprey production rate studies in Mendocino, Sonoma, and Marin Counties (including continued work on the Usal Creek population to evaluate the impact of logging).

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Literature Cited

American Birds. 1975. Kites, hawks, osprey. American Birds. 29(5):1030.
Ames, P. L. 1966. DDT residues in the eggs of the Osprey in the Northeastern United States and their relation to nesting success. J. Appl. Ecol. 3 (Suppl.): 87-97.
————, and G. S. Mersereau. 1964. Some factors in the decline of the Osprey in Connecticut. Auk 81:173-185.
Diamond, J. M. 1969. Avifauna equilibria and species turnover rates on the Channel Islands of California. Proc. Nat. Acad. Sci. U.S.A. 64:57-63.
French, J. M. 1972. Distribution, abundance and breeding status of Ospreys in northwestern California. Humboldt State Univ., Arcata, California. M.S. Thesis. v + 58 pp.
Gale, R. M., and L. D. Forbis. 1974. A Habitat Management Plan for Osprey in the Klamath National Forest. USDA For. Ser., San Francisco. 45 pp.
Garber, D. P. 1972. Osprey Study Lassen and Plumas Counties California, 1970-71. Calif. Wildl. Manage. Branch, Admin. Rep. 72-1. 33 pp.
Grinnell, J. 1915. A Distributional List of the Birds of California. Pac. Coast Avifauna No. 11. 217 pp.
————, J. Dixon, and J. M. Linsdale. 1930. Vertebrate Natural History of a Section of Northern California through the Lassen Peak Region. Mus. Vert. Zool., Univ. Calif., Vol. 35. 594 pp.
Henny, C. J. 1977. Research, management, and status of the Osprey in North America, pp. 199-222. I.C.B.P., World Birds of Prey Conf. (Vienna). 442 pp.
————, and A. P. Noltemeier. 1975. Osprey nesting populations in the coastal Carolinas. American Birds 29:1073-1079.
————, and W. T. VanVelzen. 1972. Migration patterns and wintering localities of American Ospreys. J. Wildl. Manage. 36:1133-1141.
————, and H. M. Wight. 1969. An endangered Osprey population: estimates of mortality and production. Auk 86:188-198.
————, M. M. Smith, and V. D. Stotts. 1974. The 1973 distribution and abundance of breeding Ospreys in the Chesapeake Bay. Chesapeake Sci. 15:125-133.
————, M. A. Byrd, J. A. Jacobs, P. D. McLain, M. R. Todd, and B. F. Halla. 1977. Mid-Atlantic coast Osprey populations: present numbers, productivity, pollutant contamination, and status. J. Wildl. Manage. 41:254-265.
Jewett, S. G. 1923. Ospreys in Modoc County, California. Calif. Fish and Game 9:125.
Kahl, J. R. 1971. Osprey Habitat Management Plan, Lassen National Forest. USDA For. Ser., San Francisco. 38 pp.
Lynch, J. F., and N. K. Johnson. 1974. Turnover and equilibrium in insular avifaunas, with special reference to the California Channel Islands. Condor 76:370-384.
Martin, R. O. R., and R. L. Hanson. 1966. Reservoirs in the United States. U.S. Geol. Surv., Water-Supply Pap. 1838. 115 pp.
Ray, M. S. 1915. Nesting of the American Osprey at Eagle Lake, California. Condor 17:70-74.
Sheldon, H. H. 1907. A collecting trip by wagon to Eagle Lake, Sierra Nevada Mountains. Condor 9:185-191.
Ueoka, M. L., and J. R. Koplin. 1973. Foraging behavior of Ospreys in northwestern California. Raptor Res. 7:32-38.

Appendix. California Lakes and Reservoirs Surveyed for Nesting Ospreys in 1975.

Abbott Lagoon
Alpine Lake
Baum Lake
Big Lagoon
Big Lake
Black Butte Reservoir
Bucks Lake
Butt Valley Reservoir
Clair Engle Lake
Lake Mildred
Lake Oroville
Lake Pillsbury
Little Grass Valley Reservoir
Lower Bohn Lake
McCoy Flat Reservoir
McCreary Lake
Meiss Lake
Merle-Collins Reservoir

Clear Lake
Concow Reservoir
Copco Lake (I and II)
Coyote Reservoir
Detert Reservoir
Dwinnell Reservoir
Eagle Lake
East Park Reservoir
Eastman Lake
Hog Flat Reservoir
Iron Gate Reservoir
Kent Lake
Kunkle Reservoir
Lake Almanor
Lake Berryessa
Lake Britton
Lake Earl
Lake Hennessey
Lake Mendocino
Mountain Meadows Reservoir
New Bullard Bar Reservoir
Nicasio Reservoir
Pit Four Reservoir
Rising River Lake
Round Valley Reservoir
Ruth Reservoir
Shasta Lake
Silva Flat Reservoir
Smith Lake
Snake Lake
Stone Lagoon
Stony Gorge Reservoir
Straylor Lake
Thermalito Forebay
Thermalito Afterbay
Thurston Lake
Upper Bohn Lake
Whiskeytown Reservoir

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An Analysis of the Journal Literature on Wyoming Mammals

Abstract

We searched six journals for articles on mammals in Wyoming. One hundred thirty were found to deal with 57 of the state's 104 native mammal species. Forty-eight percent of the articles were two pages or less. Elk, moose, bighorn sheep, deer mice, and western jumping mice were the mammals most studied; ecology and habitat, behavior, reproduction-genetics, and distributions were the most researched subjects. Twenty-three percent of the papers were by three of the 96 authors. Only 25 percent of the authors claimed affiliation with the University of Wyoming. Funding was attributed in 19 cases to federal agencies, 18 out-of-state, and three in-state institutions. Fifty-one percent of the studies were made in Yellowstone and Teton County (contains Grand Teton National Park); 33 percent in 16 other counties. Much needs to be learned about most Wyoming mammals.

Introduction

Wyoming contains 104 native mammal species (Hall and Kelson, 1959; Long, 1965; Maxell and Brown, 1968). There is a growing need for resource managers and others to have a good overview and ready access to the mammal literature. This need is pressing in a state such as Wyoming, which is undergoing massive environmental changes from mushrooming human populations conjoined with energy and mineral exploitation.

Methods

We searched six journals: *Journal of Mammalogy* (1919-75) had 87 papers, *Journal of Wildlife Management* (1937-75) had 20 papers, *American Midland Naturalist* (1950-75) had 5 papers, *Ecology* (1924-75) had 4 papers, *Southwestern Naturalist* (1956-75) had 7 papers, and *Northwest Science* (1927-75) had 7 papers. Other sources, such as monographs and miscellaneous or irregular publications of the U.S. Park or Forest Services, Wyoming Game and Fish Department, and historic material, were beyond the scope of our study. Other journals, such as *Behavior* and *Animal Behavior*, contain only a very few references and were not included as they were not a major publication outlet. Several theses from area universities have made their way into these six journals, and so no effort was made to include all unpublished theses.

A paper of any length was included if its main focus (at least one page) was on a species or a group of species of mammals studied wholly or mostly in Wyoming. Data recorded from each paper were: authors, title, date, residence and affiliations of authors,

sources of funding, species, subject matter, descriptive or theoretical orientation, field vs. laboratory study, and study area.

Results and Discussion

One hundred thirty articles were found to deal with Wyoming mammals. Two thirds (n = 87) were in the *Journal of Mammalogy*, which was the oldest of the six journals. Forty-eight percent were two pages or less; these 62 "notes" dealt mostly with abnormalities in individuals, previously unreported behavior, body measurements, and records of geographic distribution. Sixty-nine papers were three pages or longer and may be considered "major" studies. In 236 journal-years (total years searched for all six journals), one paper was published per 1.8 journal-years, and one major paper was published per 3.4 journal-years. The number of papers published in each 5-year period increased fairly steadily with two exceptions: 1) a noticeable drop occurred during WWII (1941-45); and 2) a sharp increase distinguished the late 1960s (1966-70) (Table 1).

TABLE 1. Distribution of Wyoming mammalogy articles by length and years.

Length	5 Year Blocks												
	1916 -20	1921 -25	1926 -30	1931 -35	1936 -40	1941 -45	1946 -50	1951 -55	1956 -60	1961 -65	1966 -70	1971 -75	Totals
≤2 pgs	2	5	5	6	1	3	9	8	4	9	5	5	62
≥3 pgs	0	1	5	2	7	2	1	5	10	5	21	9	68
Totals	2	6	10	8	8	5	10	13	14	14	26	14	130

This increase may reflect increased funding which again dropped off in the 1970s. This point could not be confirmed by the data on funding since so many papers failed to mention funding sources.

Although Long (1965) listed 101 mammal species (excluding *Homo sapiens*) in Wyoming, only 57 were "researched" in the journals and years examined (including two species not listed by Long). Thirty-nine species were the subject of only one or two papers. The most studied species were: 1) big game: elk (18 papers), moose (11), and bighorn sheep (6); 2) the ubiquitous deer mouse (8), and 3) the relatively unique western jumping mouse which hibernates about 9 months each year (7) (Table 2). Through 1930 only 14 species had been studied; by 1950, this number had risen to 32.

Some papers discussed more than one subject and a total of 142 subjects were recorded. Four subject categories received 80 percent of the research attention: ecology and habitat (23 percent), behavior (21 percent), reproduction-genetics (13 percent), and distributions (13 percent). Other subject categories were: anatomy-physiology, populations, general biology, methods, diseases-parasites, management, and taxonomy. With papers divided into eleven subject categories, it is difficult to assess trends in research. Most papers were of a descriptive nature, with a single theoretical one. One hundred twenty-eight were the result of field research and two were reports of study in the laboratory.

The 130 papers were by 96 authors. Seventy-two persons (75 percent) wrote one paper; 21 persons were authors of between two and six papers. Three authors wrote 23 percent of the papers: M. P. Skinner wrote 9 papers, T. W. Clark 10, and L. N. Brown 11. The authors' residences were listed on 72 occasions (45 percent) as Wyoming and

TABLE 2. Mammalian species studied in Wyoming and the number of papers published on each species (only species with three or more papers are listed[1]).

Order and Species	No. of Papers
RODENTIA	
Marmota flaviventris (Yellow-bellied marmot)	4
Spermophilus richardsonii (Richardson's ground squirrel)	5
Thomomys talpoides (Northern pocket gopher)	5
Peromyscus maniculatus (Deer mouse)	8
Phenacomys intermedius (Heather vole)	3
Microtus longicaudus (Long-tailed vole)	3
M. montanus (Montane vole)	3
M. pennsylvanicus (Meadow vole)	3
Zapus princeps (Western jumping mouse)	7
ARTIODACTYLS	
Cervus elaphus (Wapiti, or elk)	18
Alces alces (Moose)	11
Ovis canadensis (Bighorn sheep)	6
Antilocapra americanus (Pronghorn)	5
Odocoileus hemionus (Mule deer)	4
Bison bison (Bison)	3
CARNIVORA	
Ursus americanus (Black bear)	5
Lynx rufus (Bobcat)	3
Taxidea taxus (Badger)	3

[1]Species with less than 3 published journal articles: **Didelphis marsupials, Sorex palustris, Sorex merriami, Sorex nanus, Euderma maculatum, Myotis lucifugus, Myotis volans, Myotis evotis, Myotis subulatus, Myotis thysanodes, Ochotona princeps, Lepus townsendii, Eutamias minimus, Spermophilus tridecemlineatus, Spermophilus lateralis, Spermophilus armatus, Cynomys leucurus, Tamiasciurus hudsonicus, Sciurus aberti, Glaucomys sabrinus, Perognathus flavescens, Castor canadensis, Peromyscus crinitus, Clethrionomys gapperi, Neotoma cinera, Microtus richardsoni, Erethizon dorsatum, Canis latrans, Canis lupus, Vulpes fulva, Ursus horribilis, Bassariscus astutus, Martes pennanti, Martes americana, Mustela nigripes, Mustela frenata, Mustela erminea, Lynx canadensis, Odocoileus virginianus.**

89 times (55 percent) as outside the state. That so many authors come from other areas may reflect the scientific significance of Wyoming's mammal resources. Authors were affiliated with the University of Wyoming on only 41 occasions (25 percent) and with other universities 61 times (39 percent). Of 26 other schools listed (all in U.S.), eight were in adjacent states, and 10 were in the midwest. A large number of in-state authors were federal employees. The National Park Service was listed as the employer 29 times (12 percent), the U.S. Fish and Wildlife Service 13 times (8 percent), and Wyoming Game and Fish Department 7 times (4 percent). The U.S. Forest Service, various other state game and fish agencies, and several museums sponsored 9 others, and authors on 10 occasions did not indicate their affiliations.

One hundred papers (77 percent) did not indicate the funding source. In 40 cases where funding was determined, 19 were attributed to federal agencies, 18 to out-of-state agencies or institutions, and only 3 to in-state institutions. The many papers with no citation of funding sources may indicate casual observations and not specific research.

Wyoming has 23 counties plus Yellowstone National Park. Thirty-nine studies (30 percent) were made in Teton County (contains Grand Teton National Park) and 30 (21 percent) were in Yellowstone. Forty-three (33 percent) were done in 16 other counties, including 7 in Carbon County and 13 in Albany County. The proximity of the University of Wyoming in Laramie may account for the large number of studies in these two counties. In six counties no studies were made. Thirteen papers described their study areas as the whole state or as areas larger than a county (e.g., "southeastern

Wyoming"). Three papers focused on mammals from unspecified study areas. This journal search indicates that much remains to be learned about many native mammals in large areas of the state.

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Literature Cited

Hall, E. R., and K. R. Kelson. 1959. The Mammals of North America. Ronald Press Co., New York, 2 Vol. 1083 pp.

Long, C. A. 1965. The Mammals of Wyoming. U. Kans. Mus. Nat. Hist. Publ. 41:493-758.

Maxell, M. H., and L. N. Brown. 1968. Ecological distribution of rodents on the high plains of eastern Wyoming. Southwest. Nat. 13:143-158.

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The Sage Vole, Lagurus curtatus, as an Inhabitant of Subalpine Sheep Fescue, Festuca ovina, Communities on Steens Mountain—an Observation and Interpretation

Abstract

Suitability of sage vole, *Lagurus curtatus*, habitat in the subalpine sheep fescue, *Festuca ovina*, communities along the western slope of the crest of Steens Mountain, Harney County, Oregon, is dependent upon the structure of the erosion phase of the community. Four erosion phases are characterized, and the interrelationships of these phases to sage vole habitation is discussed.

Introduction

The purpose of this paper is to characterize the microhabitats occupied by the sage vole, *Lagurus curtatus,* on Steens Mountain in southeastern Oregon.

The western slope, between 2440-2900 m elevation, once supported extensive, floristically distinctive grass and forb communities (Griffiths, 1902; Hansen, 1956) on a variety of topo-edaphic habitats. On moderate to deep soils where snow deposition was also moderate, lush grass communities developed with *Festuca* species, particularly sheep fescue, *Festuca ovina,*[2] dominating the vegetation (Karl Urban, Pendleton, Oregon, pers. comm., 1976).

Grazing of domestic sheep, *Ovis aries,* and cattle, *Bos taurus,* began on the mountain in about 1874 (John Schaff, Burns, Oregon, pers. comm., 1977). Overgrazing resulted in severe depletion of vegetation cover by 1900 (Griffiths, 1902). In some habitats, as evidenced by early photographs, the *Festuca* was eliminated with much loss of topsoil. This event occurred on landforms that superficially appear uneroded at the present time.

Sheep numbers declined and their grazing was discontinued in 1971. Cattle grazing continues, however, and is presently managed for improvement of plant cover, particularly in habitats dominated by *Festuca ovina,* the principal forage plant in the subalpine zone.

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[2] Opinion is divided as to the identity of the *Festuca* taxa above 2500 meters on Steens Mountain. *Festuca idahoensis, ovina, and scabrella* occur in various collections, often misidentified and confused with each other or other *Festuca.* Taxonomically our material and observations indicate *ovina* is the major *Festuca* in the subalpine communities.

The sage vole, contrary to implications of its vernacular name, is not restricted to areas of sage brush, *Artemisia* spp., but is opportunistic and adaptable to a variety of habitats within a given region during years of high population or when an area has been altered by human activity to the benefit of the voles (Maser *et al.*, 1974). The latter circumstance appears to be the case on Steens Mountain. Hansen (1956:147) wrote of the 41 sage voles that he caught on Steens Mountain: "These mice were confined to the dry bunchgrass situations on the Mountain. They ranged from 9400 feet (2865 m) in somewhat rocky areas to the lower limits of that type at about 5400 feet (1646 m). The grass and not the sagebrush seemed to be the limiting factor for them. In these areas the soil was fairly loose and usually dry and deep." Although Hansen suggested that grass rather than sagebrush limited sage vole distribution, he did not discuss the vole's ecological relationship with the grass.

On 31 July 1975, fresh sage vole droppings were found at the entrance of occupied burrows (Fig. 1) at an elevation of 2895 m near the crest of the Mountain (for a more

Figure 1. Entrance of a *Lagurus curtatus* burrow dug at the base of a *Festuca ovina* pedestal on Steens Mountain. Note the feces and cut grass stems below the entrance. August 1975.

detailed discussion of sage vole sign see Maser *et al.*, 1974:203-204). Shortly thereafter a sage vole was caught in a snap trap. Subsequent trapping and observations on slopes west of the crest, between 2743 and 2926 m, showed that sage voles were primarily in *Festuca*-dominated communities, but their abundance and activity in these communities varied considerably, apparently with differences in ground surface configurations as a result of soil erosion.

We have categorized these configuration differences into four phases of erosion for convenience in relating the vole's association with specific surface features and vegetation. The phases reflect in some respects the soil erosion and plant successional stages established by Pickford and Reid (1942) during their studies of similarly eroded subalpine grasslands in the Wallowa Mountains in northeast Oregon, but without quantitative data, we make no such classifications of our phases. Instead they are merely descriptive of the non-eroded and eroded surface soils and the associated plant communities. The phases are Phase I. Non-eroded continuous sod; Phase II. Eroded sod; remnant topsoil in closely spaced pedestals and larger mesa-like sods (hummocks); Phase III. Eroded sod; remnant topsoil in small, widely-dispersed pedestals, and Phase IV. All topsoil sod eroded from the site.

Discussion

The Festuca Communities

Large areas of Phase I are not common on Steens Mountain because of the extensive soil erosion. Our only example of this Phase was a continuously sodded, *Festuca ovina*-dominated plant community (Fig. 2) above the head of Little Blitzen Gorge. Large boulders and stones were abundant and embedded in the sod, a feature which may have prevented excessive grazing and subsequent erosion. The surface soil between *Festuca* plants was loose and friable yet appeared uneroded; the surface gravel common to eroded

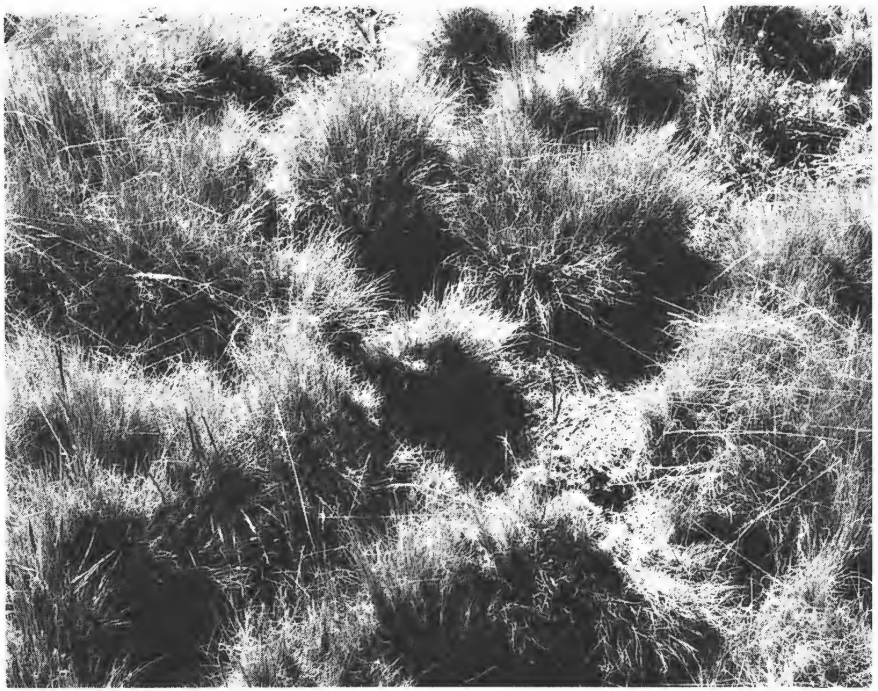

Figure 2. Uneroded *Festuca ovina* sod, Phase I, on Steens Mountain. August 1975.

phases was absent. In addition, the crowns of the closely spaced *Festuca* were only slightly raised above the general land surface, indicating little if any active erosion.

In contrast, erosion Phase II and III exhibit the universal characteristic of eroded subalpine grasslands: the restriction of *Festuca* plants to growth on remnant topsoil pedestals and hummocks elevated 10 to 20 cm or more above an eroded surface. The soil in these topsoil blocks is bound and held in place by the dense, fibrous grass roots.

The differences in Phase II and III configurations are in size, density, and distribution of the pedestals and hummocks. In Phase II, they are generally >10 cm in height, 15 cm or more in diameter, and closely spaced, having the general appearance of a deeply dissected soil (Fig. 3). Phase III appears as a more eroded Phase II with a loss in pedestal numbers (Fig. 4). Thus, it has the general appearance of a gravelly, uniform land surface studded with shorter, smaller, and more widely dispersed soil pedestals.

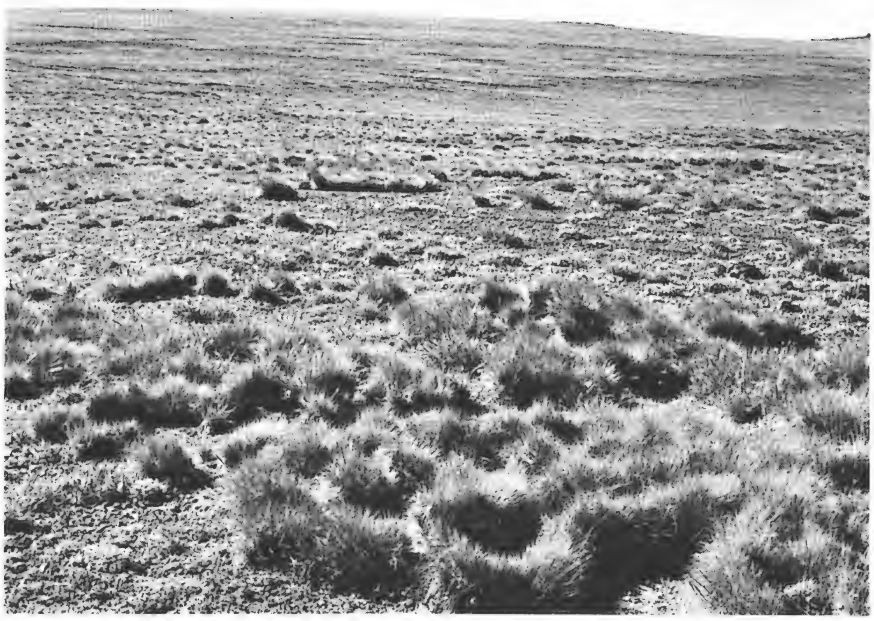

Figure 3. Eroded *Festuca ovina* communities on Steens Mountain. The Phase II configuration on a uniform land surface is in the foreground with Phase III beyond. August 1975.

Phase II is common on relatively large "mima-like" mounds of deep, non-stony soils elevated 30 to 60 cm above surrounding land surfaces. Because of the vigorous *Festuca* plants growing on the pedestals, these mounds appear as bright green islands, several square meters in area, in the duller green vegetation of more shallow soils.

On uniform, non-mounded land surfaces with less soil depth, the erosion pattern trends toward the Phase III configuration with pedestals smaller in cross section and height (<10 cm) and a gravelly surface in the eroded interstices. However, on such

Figure 4. Phase III erosion configuration on Steens Mountain, characterized by widely dispersed pedestals on a gravel covered surface. August 1975.

surfaces Phase II still persists, particularly where closely spaced pedestals are interspersed with sodded hummocks up to 1 sq m in area (occasionally larger). *Festuca ovina* is commonly established on these hummocks as a continuous or broken ring of plants around the periphery; the hummock centers are either of matted litter from dead *Festuca* tillers and crowns or of loose, friable soil. In the latter case, the underlying root mass has died and erosive processes have continued as evidenced by a concave microrelief within the *Festuca* ring. The grass roots often die and break down, accompanied by erosion of the *Festuca* ring itself. This occurrence results in a ring-like series of pedestals, all or some of which are occupied by *Festuca* or other plants, but one or more pedestals are generally without any live plant growth. Such a degree of hummock breakdown is normally associated with the Phase III configuration.

Phase IV, where all topsoil has eroded off the site, is recognized by the occasional pedestal of remnant topsoil on a uniform land surface paved with gravels and small stones (Fig. 5). Without identifying pedestals (or other remnant sods), eroded sites are difficult to separate from uneroded sites on shallow, stony soils. The latter, however, generally have larger stones and show no gravelly erosion pavement.

Rate of breakdown of pedestals and hummocks from Phase II to Phase IV is controlled by several factors. Studies on other eroded *Festuca* grasslands (Gerald Strickler, unpub. data) show *Festuca* growth to be limited and cyclic on the pedestals and hummocks. Growth is thought to be controlled not only by physiological limits of *Festuca* plant-size but also by physical limitations of space and available soil moisture because

of the plants' elevated position on the topsoil remnants. In good moisture years, tillers of *Festuca* appear and eventually coalesce in the center of the hummock, only to die back again in dry years. Moreover, tiller vigor and density of peripheral plants generally decrease during dry years.

Continued grazing and trampling by livestock, burrowing and feeding by gophers and voles, coupled with wind and water erosive processes, can speed the desiccation and breakdown of the pedestals. On the other hand, vigorous *Festuca* or other long-lived plants can maintain pedestal shape and structure for more than 30 years.

The plant communities of all Phases, except IV, are dominated by grasses and grass-like species but mainly by *Festuca ovina.* In the uneroded Phase I, the *Festuca* plants are large, up to 38 cm in diameter, and closely spaced; in the eroded phases, size and spacing, as previously described, are controlled by pedestal size and distribution.

Figure 5. Eroded *Festuca ovina* community on Steens Mountain. Phase IV, where all topsoil has been eroded away, is in the foreground. Small areas of Phases II and III erosion are seen beyond. August 1975.

Prairie junegrass, *Koeleria cristata,* dunhead sedge, *Carex phaeocephala,* and several species of bluegrass, (*Poa scabrella, fendleriana, cusickii,* and *sandbergii* complex), are found in and between the *Festuca* plants on all Phases, but are more abundant in Phase I. Rough fescue, *Festuca scabrella,* was observed only in the Phase I community and bottlebrush squirreltail, *Sitanion hystrix,* only in the eroded phases. Both can undoubted-

ly occur, however, in all phases, as observed in other subalpine grasslands. Numbers of *Sitanion hystrix* increased as erosion increased. It was the most abundant grass in some Phase III communities and the only grass in some Phase IV communities.

A large number of forbs are conspicuous on Steens Mountain; the forb component is of insufficient abundance or stature to distract from the *Festuca* dominance of most communities until the late Phase III and Phase IV configurations occur.

On the non-eroded Phase I, common forbs were silky phacelia, *Phacelia sericea,* skunkleaf polemonium, *Polemonium pulcherrimum,* dwarf mountain fleabane, *Erigeron compositus,* western yarrow, *Achillea millefolium,* varileaf cinquefoil, *Potentilla diversifolia,* manystalked clover, *Trifolium multipedunculatum,* and woodlandstar, *Lithophragma* sp. Of these, the *Erigeron* and particularly the *Trifolium* increase in abundance in the eroded phases, whereas many of the others are absent.

In Phase II, *Trifolium multipedunculatum,* prairie lupine, *Lupinus lepidus lobbii,* and dandelion, *Taraxacum* sp., are the common forbs associated with *Festuca* on the deep soil mounds. However, they are generally restricted to the bases of the pedestaled root masses. On the shallower, uniformly eroded surfaces, *Trifolium* forms large patches and *Lupinus* and *Taraxacum* increase in density. Umbellate pussypaws, *Spraguea umbellata,* spreading phlox, *Phlox diffusa,* and lanceleaf stonecrop, *Sedum lanceolatum,* become conspicuous—*Spraguea* on the eroded surfaces and the *Phlox* and *Sedum* around the periphery of pedestals and stones.

These same forbs are common to abundant in similar situations in Phase III and IV. *Trifolium* and *Lupinus* attain maximum coverage in these Phases, often dominating large areas of the gravelly, eroded surfaces. With *Sitanion hystrix*, they are the common dominants in Phase IV communities, although *Festuca ovina*, where re-established on the eroded soil, may dominate localized areas of several square meters. Total plant cover is usually low and composed of many species on both Phase III and IV erosion surfaces. Of the 30 species listed as common to the shallow, barren bunchgrass habitats by Hansen (1956), we noted, in addition to those listed above, that needleleaf sandwort, *Arenaria aculeata,* and Gordon ivesia, *Ivesia gordonii,* were conspicuous around boulders and rock outcrops. On the other hand, dwarf mountain groundsel, *Senecio fremontii,* and (occasionally) sneezeweed, *Helenium hoopesii,* were on the gravelly, loose soils.

The Vole

Sage voles are primarily inhabitants of Phases I and II, but as a vole population-cycle increases, population pressures force individuals to occupy Phase III. Such occupancy, however, is largely dependent upon the availability of abandoned gopher (*Thomomys talpoides*) burrow systems because the soil is too hard for the voles to dig through (Maser *et al.*, 1974).

On Steens Mountain, Phase I probably acted as a reservoir from which sage voles dispersed (easily under cover of snow) to areas in which Phase II developed (and is developing) after livestock grazing was reduced. To date, sage voles are more generally distributed throughout Phase I than they are in Phase II because the lack of continuous, protective cover surrounding Phase II acts to concentrate them within its confines (see Fig. 3). Contours of the closely spaced topsoil pedestals form natural, protected runways which protect the voles from the almost constant wind and moderate temperature fluctuations (Table 1). The pedestals themselves form sites into which the voles can dig and construct their nests. In addition, the pedestals' elevated nature tends to keep

the voles' nests above the level of spring runoff as snow melts. Furthermore, the elevated pedestals speed early melting of snow with corresponding growth of vegetation which is important to the voles in spring (Maser *et al.*, 1974).

TABLE 1. Temperature relationships within a Phase II **Festuca ovina** community at 2926 m on Steens Mountain, 3-4 August 1975.

Time[1]	Temperature	
	Open eroded surface	Between soil pedestals
	Centigrade	
August 3		
1330	40.0[2]	31.1[2]
1515	31.1	28.3
1900	16.7	15.6
1930	10.0	10.0
August 4		
	-3.3[3]	-
0530	-1.1	1.1

[1] Mountain Standard Time
[2] Maximum day temperature
[3] Minimum night temperature

In addition to cover and reproductive habitat, *Festuca ovina* Phases I, II, and at times III are sage vole feeding habitat; the voles feed within and next to the *Festuca* plants. During the first week of August 1975, the most important foods were leaves, culms, and green seeds of *Festuca ovina.* Other plants eaten were leaves, culms, and green seeds of *Sitanion hystrix*, leaves and stems of *Trifolium multipedunculatum*, and leaves of *Taraxacum officinale.* Maser *et al.* (1976) also found that the hypogeous mycorrhizal fungus, *Glomus fasciculatus* (Endogonaceae), formed 1 percent of the stomach contents by volume with 25 percent frequency of 16 sage vole stomachs from the Phase II *Festuca ovina* community on Steens Mountain. Moreover, Dowding(1955) reported finding spores of *Glomus fasciculatus* in the stomach of a sage vole from southeastern Alberta, Canada.

The Interrelationship

Under most circumstances, sage voles occupy a particular habitat with a variety of small mammals. On the crest of Steens Mountain, however, the sage vole—and occasionally the pocket gopher—appears to be the sole small mammal in most Phase II *Festuca ovina* communities. As such, the interrelationships between the voles and the *Festuca* assume greater significance.

The *Festuca ovina* community (Phases I, II, and sometimes III) gives the sage voles a habitat for reproduction and for feeding. In turn, the voles' apparent dependence upon the *Festuca* sod and pedestals, especially in Phase II, concentrates their waste products in and around the grass. Sage voles cut far more vegetation than they eat and also produce large quantities of fecal pellets, both of which are deposited in and around the *Festuca* plants. The food refuse, feces, and urine make nutrients available to the *Festuca* plants, and the fecal pellets contain viable spores of *Glomus fasciculatus* (Maser *et al.*, 1978; Trappe and Maser, 1976)—an obligatory symbiotic hypogeous fungus that forms a mycorrhizal association with the roots of the *Festuca* (Randy Molina, Corvallis, Oregon, pers. comm., 1977). So, while the voles are dependent upon the *Festuca*—particularly Phase II—the *Festuca* also benefits from the voles' waste products and the inoc-

ulum of viable spores of the mycorrhizal-forming fungus necessary to the health and growth of the grass. In addition, the cyclic "behavior" of *Festuca* on the hummocks and pedestals may be modified and/or prolonged by the voles' burrowing and feeding habits. Such a relationship would maintain, over time, suitable habitat for the voles in an otherwise unsuitable area—the relatively windswept crest of Steens Mountain.

Conclusion

The mosaic of erosion surfaces on the crest of Steens Mountain provides numerous examples of suitable and unsuitable habitat for sage voles. As is often the case, it took interdisciplinary expertise to interpret the ecological observations. Without such interpretation we may not understand the plant-animal community interrelationships necessary to the art of predicting the effects of habitat manipulation (management) upon the attendant wildlife.

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Literature Cited

Dowding, E. S. 1955. *Endogone* in Canadian rodents. Mycologia 47:51-57.

Griffiths, D. 1902. Forage Conditions on the Northern Border of the Great Basin, Being a Report upon Investigations Made During July and August, 1901, in the Region between Winnemucca, Nevada, and Ontario, Oregon. U.S. Bur. Plant Ind. Bull. 15, 60 pp.

Hansen, C. G. 1956. An Ecological Survey of the Vertebrate Animals on Steen's Mountain, Harney County, Oregon. Oregon State College, Corvallis. Ph.D. Thesis. 199 pp.

Maser, C., E. W. Hammer, C. Brown, R. E. Lewis, R. L. Rausch, and M. L. Johnson. 1974. The sage vole, *Lagurus curtatus* (Cope 1868), in the Crooked River National Grassland, Jefferson County, Oregon. A contribution to its life history and ecology. Säugetierk. Mitt. 22:193-222.

———, J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology (in press).

Pickford, G. D., and E. H. Reid. 1942. Basis for Judging Subalpine Grassland Ranges of Oregon and Washington. U.S. Dept. Agric. Cir. 655. 38 p.

Trappe, J. M., and C. Maser. 1976. Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. Mycologia 68:433-436.

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Upper Lethal Water Temperature Levels for English Sole (Parophrys vetulus) and Rock Sole (Lepidopsetta bilineata) Subjected to Gradual Thermal Increases

Abstract

Comparative studies of the relative tolerance of 483 English sole and 260 rock sole to thermal stress are described in the following report. Test animals were taken from Puget Sound, Washington, and ranged in size from 80 to 360 mm. The test procedure was to start at ambient water temperature and (1) gradually raise the temperature during the first hour; (2) hold a "test" temperature for the next 4 hours, and then (3) gradually reduce the temperature to the ambient level during the last (sixth) hour. Test temperatures of either 18, 21, 24, or 27°C were reached during the six-hour period. Each test was followed by a seven-day observation period to determine delayed mortalities.

The lethal level at which 50 percent of the fish survived (LL50) was 26.1°C for English sole and 24.9°C for rock sole during the 27°C test. The LL50 was not reached at any other test temperature.

Total mortalities were 20 percent for English sole and 35 percent for rock sole. Within these totals, approximately 60 percent mortality occurred during the observation or delay period for both species. Individuals most susceptible to elevated temperatures were the larger and smaller fish rather than those of intermediate size.

Introduction

The effect of alterations in the marine environment is of prime consideration in managing fish and shellfish resources. Perhaps even more critical are marine areas of relative confinement—such as Puget Sound, Washington— in comparison with open coastal ecosystems. An increase in population growth of the Puget Sound region may lead to the construction of nuclear electric power plants; this event would raise the possibility of increased water temperatures caused by thermal effluents from the plants.

Fifteen species of flatfish have been reported for the Port Gardner area (off Everett, Washington) of Puget Sound (Delacy, Miller, and Borton, 1972). The most important commercially are English sole, *Parophrys vetulus*, and rock sole, *Lepidopsetta bilineata* (English, 1967). The latter species is the most utilized of smaller flatfish in adjacent waters of British Columbia (Hart, 1973). A total of 5½ million pounds of flatfish were landed in 1972 in Puget Sound; these fish were caught in Puget Sound and adjacent coastal waters of Washington and British Columbia, and nearly half of this total were English and rock sole (Ward *et al.*, 1972).

Laboratory studies of simulated effects of man-made thermal extremes have been documented for numerous freshwater fishes and invertebrates. Much less thermal research has been done on marine species. Behavioral experimentation by Yocum and

Edsall (1974) showed decreased resistance to predation in lake whitefish, *Coregonus clupeaformis*, as a result of thermal elevations. The ability of certain competitors to withstand temperatures that stress juvenile salmonids was demonstrated by Blahm and Parente (1970). Alderdice and Forrester (1968; 1971a; and 1971b) and Ehrlich and Farris (1970) described effects of temperature and temperature-salinity synergy on certain developmental stages of fishes. Somero and Hochachka (1971) discussed seasonal temperature variations and corresponding "biochemical restructuring" which normally occurs in certain adult fishes. Houston (1971) described the effects of undue alterations in the thermal environment with respect to homeostatic mechanisms in fishes. Bush, Welch, and Mar (1974) compiled an estimate of response to thermal alterations for fish and invertebrate communities in six representative river systems in the United States.

The purpose of this report is to make comparative observations on the gross effects of gradual thermal elevations on English and rock sole. Determinations are made showing the relationship of mortality to fish size, temperature regimes, and seasonal periods.

Methods and Materials

Totals of 483 English and 260 rock sole were subjected to laboratory tests at the Mukilteo, Washington, facility of the Northwest and Alaska Fisheries Center of the National Marine Fisheries Service. All test fish were captured in Port Gardner by otter trawl of the type described by Ellis and Stockley (1970). Both species represented a relatively broad size range excluding the young of the year. English sole ranged in length from 89 to 342 mm, whereas rock sole were 88 to 335 mm. Mean lengths were 185.5 and 192.6 mm, respectively. Information on the weight and sex of individual fish was not collected.

The major components of test equipment were the rectangular fish-holding tanks, a continuous flow saltwater system, and equipment to heat salt water and monitor its temperature. Holding tanks measured 55.9 x 40.6 x 43.2 cm; construction was of fiber glass lined plywood with frontal glass observation port. A 35-cm standpipe allowed a volume of 75 liters of flow-through water. The continuous flow saltwater system supplied water to the test facility at a rate of 380 liters (100 gallons) per minute. The inlet of the system was approximately 60 m (180 ft) from shore, at a mean depth of 10 m (30 ft). Ambient temperatures were monitored at the inlet by means of a Bristol[1] single pen thermograph and in the laboratory by means of a Hydrolab model 6D with model 70 sonde. Average ambient water temperatures varied $\pm$ 1.3°C between the inlet and the laboratory. A 40 kilowatt Chromalox heat-exchange unit was used to heat salt water in the retangular test tanks. Desired water temperatures (ambient and test temperatures of 18, 21, 24, and 27°C) were produced by manipulation of hot and cold water valves at each tank.

Each month from September 1972 through November 1973, thermal stress bioassay tests were conducted alternately on either English or rock sole. Prior to testing, these fish were acclimated at ambient water temperature—which during the period of testing varied from 6.9 to 13.9°C. Generally, three to eight fish, depending on individual sizes and numbers available, were tested per tank. An individual test, consisting of five different temperatures, might utilize 15-45 fish. Test temperatures were monitored frequently; compensations for fluctuations in temperature, which generally ranged no more

[1]Reference to trade name(s) in this publication do(es) not imply endorsement of commercial products(s) by the National Marine Fisheries Service, NOAA.

than $\pm 0.1°C$, were made accordingly. In an attempt to simulate a six-hour tidal cycle, temperatures were raised gradually during the first hour and gradually decreased to ambient temperature during the fifth hour. Observations of the test fish were made routinely at 30-minute intervals and more frequently during critical stress periods. All test fish were held for a seven-day observation period beyond the six-hour test, during which time signs of overt stress and delayed mortality were recorded.

Detection of stress and mortality is more difficult in some demersal types of fish—such as English and rock sole—and flatfish in general than in most pelagic types of fishes. Flatfish in captivity generally exhibit little activity at ambient temperatures and may continue in this manner during the onset of stress temperatures.

The first noticeable sign associated with thermal stress was the appearance of strings of dark slime. The exact origin of secretion is not yet known, but observations suggest some association with the opercular area.

Advanced stress was noted by increased respiration (opercular movements). In addition, certain swimming movements became more exaggerated. Rippling of the peripheral fins and arching of the body sometimes occurred. The fish made an occasional attempt to escape thermal increases by swimming to the surface and thrashing about. Gradual swimming to the surface to gulp air was also observed. After surfacing there might have been a loss of equilibrium during descent to the bottom, causing the fish frequently to land ventral side up.

The main criterion for establishing death during a thermal test was complete cessation of opercular movement.

Delayed mortality in this study was defined as mortality occurring between termination of the six-hour test and the end of the seven-day observation period.

Results of Thermal Tests

We examined and compared between species the mortality within temperature groups, the lethal level at which 50 percent of the test fish survived (LL50), mortality within length groups, and mortality within seasonal periods. Total difference in survival between the species was 15 percent (Table 1). This figure included mortalities during the

TABLE 1. Percentage mortalities of English and rock sole at ambient and test temperatures.

Species	Ambient and test temperature	Total no. of fish tested	No. of fish at termination of test and holding period		Percentage mortality
			Alive	Dead	
English sole	Amb.*	95	80	15	15.8
	18.0	94	83	11	11.7
	21.0	98	86	12	12.2
	24.0	96	76	20	20.8
	27.0	100	63	37	37.0
		483	388	95	19.7
Rock sole	Amb.	54	45	9	16.7
	18.0	54	44	10	18.5
	21.0	52	39	13	25.0
	34.0	50	31	19	38.0
	27.0	55	13	42	76.4
		265	172	93	35.1

* During 1973, ambient temperatures ranged from 6.9 to 13.9°C.

actual test and the post-test holding period. Interspecies tolerance within all temperature groups consistently favored English sole. Variation in mortality between the two species ranged from 6.8 percent at 18.0°C to 17.2 percent at 24.0°C. Between 24 and 27.0°C, rock sole mortality accelerated rapidly to 76.3 percent, whereas English sole mortality increased to only 37.0 percent (Fig. 1).

Mortality during the seven-day holding period was very nearly the same for both species (Table 2). Considering total mortalities, over 60 percent of the stressed fish

TABLE 2. Comparison of mortalities of English and rock sole during test (6 hours) and holding periods (7 days).

Species	Total mortality (no. of fish)	Mortality during test		Mortality during holding period	
		No.	Percentage	No.	Percentage
English sole	121	37	30.6	84	69.4
Rock sole	109	42	38.5	67	61.5

died during the delay period.

The lethal level at which 50 percent of the test fish survived occured only in the 27.0°C test for both species. Figure 2 shows 50 percent survival occurring at 24.9°C for rock sole and 26.1°C for English sole during the period of elevated test temperatures.

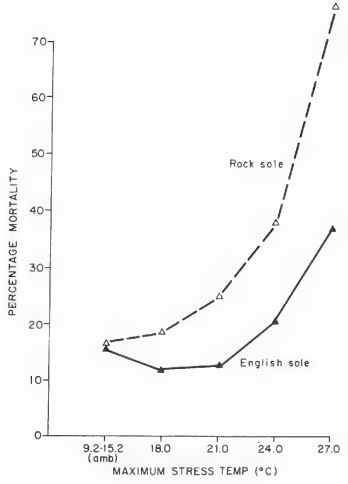
Death caused by thermal stress for both English and rock sole was highest at each extreme of the respective size ranges (Fig. 3). Within the 80-119-mm groups, mortality was about 40 percent for English sole and 60 percent for rock sole. Mortalities decreased in the median size ranges for both species. For lengths beyond 280 mm, thermal tolerance again decreased. Within sole groups greater than 280 mm in length, mortalities rose to about 50 percent for rock sole and 35 percent for English sole. Although the trend for success in thermal resistance again favored English sole, when analyzed by length groups, a single unexplainable exception occurred within the 240-279-mm group. Rock sole survival within this group slightly exceeded that of English sole.

Mortality rates for both species appeared to be somewhat independent of seasonal water temperature fluctuations. Peak acclimation (ambient) temperatures in 1973, based on monthly averages, occurred in June and July. Peak mortality for rock sole (49.3 percent) occurred in May and for English sole (46.7 percent) in August (Fig. 4) when average ambient temperature levels were in the upper 50 percent of the range. Because different results might have been expected in a test situation, based on other research, it was assumed that something other than acclimation temperature was responsible for the resultant peak mortalities.

Control groups for both species had higher mortality than expected (Table 3). Al-

TABLE 3. Percentage mortalities of control groups of English and rock sole, by length groups and upper and lower temperature ranges.

Species	Length group (mm)	Percentage mortality	
		6.9-9.5°C	9.8-13.9°C
English sole	80-119	5.8	20.4
	200-360	1.9	4.5
Rock sole	80-119	0.0	21.2
	200-360	0.0	6.0



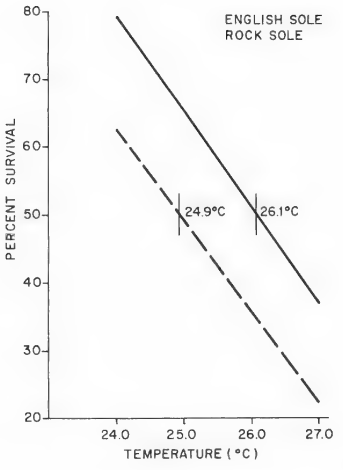
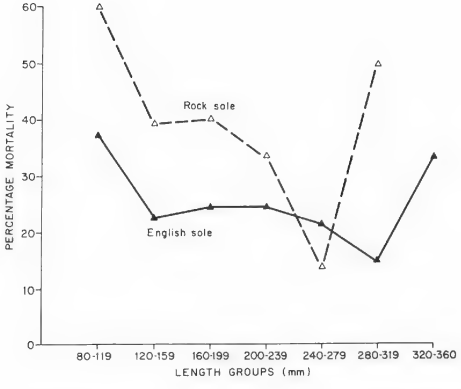


Figure 1. Comparative percentage mortalities between English and rock sole at five test temperatures. Figure 2. Comparative LL50 for English sole and rock sole held at 27°C.



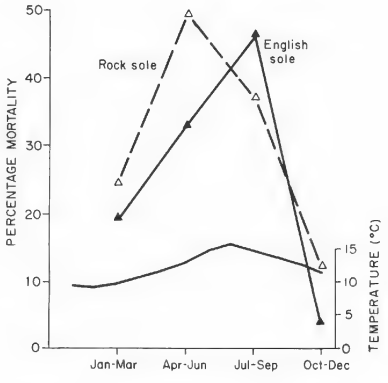


Figure 3. Percentage mortalities for English and rock sole within length groups. Figure 4. Percentage mortalities for English and rock sole within seasonal periods.

though some of the mortalities might have been attributed to capture and handling stress, the evidence indicates that it was mainly caused by seasonal ambient temperature changes and a probable effect on post-spawning state of fitness. During summer, when ambient water temperatures rose from 9.8 to 13.9°C, control group mortalities noticeably increased. This increase was much greater for small flatfish (80-119 mm) than for medium and larger fish (200 mm) of both species. These findings suggest that even temperatures in the ambient range may cause stress. Such conditions are probably avoided in the natural environment by migration to areas not influenced by thermal elevations.

Discussion

Our tests indicate that English sole were better able to withstand thermal stress than rock sole. These findings are generally consistent with the work of Stober and Salo (1972) who determined that an analogous situation under test conditions existed among juveniles of the same species during the summer at Kiket Island. Results of our study imply that in a marine environment, subject to undue thermal extremes, temperatures beyond 27°C would be considered lethal among populations of rock sole, whereas English sole would suffer only half as great a loss (less than 50 percent), comparatively. Because immature flatfish are associated with relatively shallow intertidal areas, a sudden introduction of warm water (over 24°C) would certainly have a substantial effect on that segment of the population. In deeper waters it seems likely that avoidance of a heated thermal plume by larger flatfish would be possible.

Because it has been determined for both species that over 60 percent of the flatfish deaths in laboratory tests occurred as delayed mortalities, it is assumed that certain other sublethal intrinsic changes might have taken place.

Summary

(1) Totals of 483 English sole and 260 rock sole from Port Gardner, Washington, were subjected to laboratory thermal stress tests in continuous flow sea water that was gradually raised to test temperature during a one-hour period, held at test temperature for four hours, and then decreased to ambient temperature during the final (sixth) hour.

(2) Peak mortalities of 76.3 percent for rock sole and 37.0 percent for English sole were the result of exposure to 27°C during the test period. An LL50 was determined for only the 27°C test group because of the relatively short duration of the test.

(3) About 60 percent of the total mortalities for both species occurred as "delayed" mortalities, that is, occurring during the seven-day observation period following the actual stress period.

(4) Comparison of mortalities by length groups showed test animals in the 120-280 mm range to be more temperature tolerant than individuals in the extreme length groups.

(5) Higher than expected control group mortalities for both species may possibly be associated with: (a) post-spawning period fitness; (b) periods of stress associated with higher ambient temperatures; and (c) capture and handling stress and/or a combination of any two of the aforementioned.

(6) Continuing studies are planned for thermal stress tests of the complete life cycle of both species in addition to thermal effects of maturity and reproduction.

Literature Cited

Alderdice, D. F., and C. R. Forrester. 1968. Some effects of salinity and temperature on early development and survival of the English sole (*Parophrys vetulus*). J. Fish. Res. Board Can. 25: 495-521.

————, and ————. 1971a. Effects of salinity and temperature on embryonic development of the petrale sole (*Eopsetta jordani*). J. Fish. Res. Board Can. 28:727-744.

————, and ————. 1971b. Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board Can. 28:883-902.

Blahm, T. H., and W. D. Parente. 1970. Survival of Juvenile Chum Salmon Exposed to Elevated Temperatures in Columbia River Water. Unpubl. manuscr. [U.S.] Dep. Inter., Bur. Commer. Fish., Biol. Lab., Seattle, Wash. 11 pp. (Processed.)

Bush, R. M., E. B. Welch, and B. W. Mar. 1974. Potential effects of thermal discharges on aquatic systems. Environ. Sci. Technol. 8:561-568.

DeLacy, A. C., B. S. Miller, and S. F. Borton. 1972. Checklist of Puget Sound Fishes. Univ. Wash., Seattle, Div. Mar. Resour., Sea Grant Program WSG 72-3. 43 pp. (Processed.)
Ehrlich, K. F., and D. A. Farris. 1970. Effect of temperature on number of myomeres in newly hatched grunion (*Leuresthes tenuis*). Copeia 1970 :774-775.
Ellis, I. E., and C. Stockley. 1970. Otter trawling introduced to Columbia River smelt fishery. Commer. Fish. Rev. 32:51-60.
English, T. S. 1967. Preliminary assessment of the English sole (*Parophrys vetulus*) in Port Gardner, Washington. J. Water Pollut. Control Found. 39:1337-1350.
Hart, J. L. 1973. Pacific Fishes of Canada. Fish. Res. Board Can., Bull. 180. 740 pp.
Houston, A. H. 1971. Some comments upon acid-base balance in Teleost fishes and its relationship to environmental temperature. Comp. Biochem. Physiol. 40:535-542.
Somero, G. N., and P. W. Hochachka. 1971. Biochemical adaptation to the environment. Am. Zool. 11:159-167.
Stober, Q. J., and E. O. Salo (eds.). 1973. Ecological Studies of the Proposed Kiket Island Nuclear Power Site. Univ. Wash., Seattle, Coll. Fish., Fish. Res. Inst., FRI-UW-7304, 537 pp. (Processed.)
Ward, D., R. Robison, G. Nye, and D. Reed. 1972. 1969 Fisheries Statistical Report. Wash. Dep. Fish., Olympia, Wash., 92 pp.
Yocum, T. G., and T. A. Edsall. 1974. Effect of acclimation temperatures and heat shock on vulnerability of fry of lake whitefish (*Coregonus clupeaformis*) to predation. J. Fish. Res. Board Can. 31:1503-1506.

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Distribution and Survival of Mallards Banded at Malheur National Wildlife Refuge[1]

Abstract

Distribution in time and space and survival were determined from 4385 recoveries of mallards (*Anas platyrhynchos*) banded at Malheur National Wildlife Refuge (Malheur NWR) between 1929 and 1971. Two populations of mallards using Malheur were identified. A wintering population was present in fall and winter; these mallards were a small segment of the mallard population that wintered in the Columbia Basin. A transient population was present in spring (March to May) and late summer (July to October), and apparently included mallards breeding at Malheur NWR. This population migrated to the Sacramento Valley, California, in winter (November-January). Most of the harvest of the transient population occurred in California in winter and the proportion of the harvest occurring in California increased from the 1930s to the 1960s. Survival of immature males of the transient population was low (0.377), but survivial of immature females was high (0.569); adults survived at about the continent-wide average for adult mallards. The transient population using Malheur NWR is a distinct subunit of the mallard population present in Eastern Oregon during summer and fall.

Introduction

Malheur Lake was established as a National Bird Refuge in 1908 and designated as Malheur National Wildlife Refuge (Malheur NWR), with the addition of surrounding marshlands, in 1935 (Brimlow, 1951). Primary management objectives were and remain the provision of habitat for nesting, migratory, and wintering waterfowl and other marsh birds. Previous waterfowl research centered around life history and reproductive ecology of ducks and geese (Sooter, 1938, 1940; Erickson, 1948; Jarvis and Harris, 1967, 1971). However, the relationship between populations of waterfowl using Malheur NWR and regional and flyway populations remains poorly understood. Our specific objectives were: (1) to delineate populations of mallards using Malheur NWR; (2) to characterize each population by the distribution in space and time of recoveries, and, where possible, by survival rates; and (3) to determine changes in recovery distributions between 1930 and 1972.

The waterfowl banding program at Malheur NWR began in 1926 and has continued to the present; a hiatus occurred in the 1950s when few waterfowl were banded. A total of 33,604 usable records of mallards banded between 1929 and 1971 were available for analysis. These records contained 4385 recoveries due to hunting mortality and it is these recoveries we analyzed.

Methods

The analytical framework consisted of examining recoveries by decade of recovery (1930s, 1940s, and 1960s), by season of banding (preseason, inseason, postseason, and

[1]Oregon Agricultural Experiment Station Technical Paper No. 4386.

spring), by age and sex, and by years of survival before recovery (direct and indirect). We defined "direct recoveries" as those recoveries that occurred prior to completion of the first spring migration following banding. Thus only mallards banded preseason and inseason yielded direct recoveries. We divided the year into four segments, based on the hunting season, in which banding occurred: (1) preseason, 2 July to 14 October; (2) inseason, approximately 15 October to 31 December; (3) postseason, about 1 January to 18 February; and (4) spring, 19 February to 6 May. Dates of the waterfowl hunting season varied annually and recoveries were assigned to banding periods (preseason, inseason, or postseason) based on the hunting season (before, during, or after) rather than on the calendar date of banding.

Population units were delineated on the basis of geographic and chronologic distribution of recoveries and further characterized by calculation of annual survival rates. Geographic distribution patterns were analyzed by examining the distribution of recoveries in 12 reference areas grouped into 5 reference units (Fig. 1). Chronologic distributions were analyzed by examining distribution of recoveries by 14 day periods. The Chi-square test of independence was used to test for differences in geographic and chronologic distributions. Estimates of annual recovery rates and survival rates were obtained using the method developed by Robson and Brownie (1973), Brownie (1973) and Brownie and Robson (1974). Of the three models available, we used model H_1, which assumes that recovery rates and survival rates were time-specific and age-specific; calculations were conducted independently for male and female mallards. Differences in survival and recovery rates were analyzed with Z tests. The 5 percent significance level was used in all statistical tests, unless otherwise noted.

Results

Geographic Distribution of Recoveries

Analysis of geographic distribution of indirect recoveries by season of banding, and within decade of recovery and sex, indicated basically two population units (Tables 1, 2, and 3). The two units were best represented by mallards banded preseason which had the greatest rate of recovery from Harney Basin and northward. The first population unit we have labeled a transient population; it was probably composed of mallards present during the breeding season in the Harney Basin and mallards that reproduced north of Malheur NWR but migrated to Malheur NWR prior to early October. The second unit (banded postseason) appeared to be mallards for which Malheur NWR was a terminal wintering area. Birds banded in spring were most similar in geographic distribution to mallards banded preseason and birds banded inseason were most similar to mallards banded postseason.

Age determination at the time of banding was considered to be reliable only for mallards banded preseason and recovered in 1961-1971, and hence only this cohort could be examined for effects of age on geographic distribution. Immature males were recovered at a significantly greater rate in the Harney Basin and at a lower rate south of the Harney Basin than adult males ($X^2 = 31.62$; $df = 10$) (Table 4). The same pattern also occurred in adult and immature females but was non-significant ($X^2 = 13.46$; $df = 9$).

The grouping of the 12 reference areas into 5 units obscured the highly localized distribution of most recoveries. In the six samples of mallards banded preseason and in

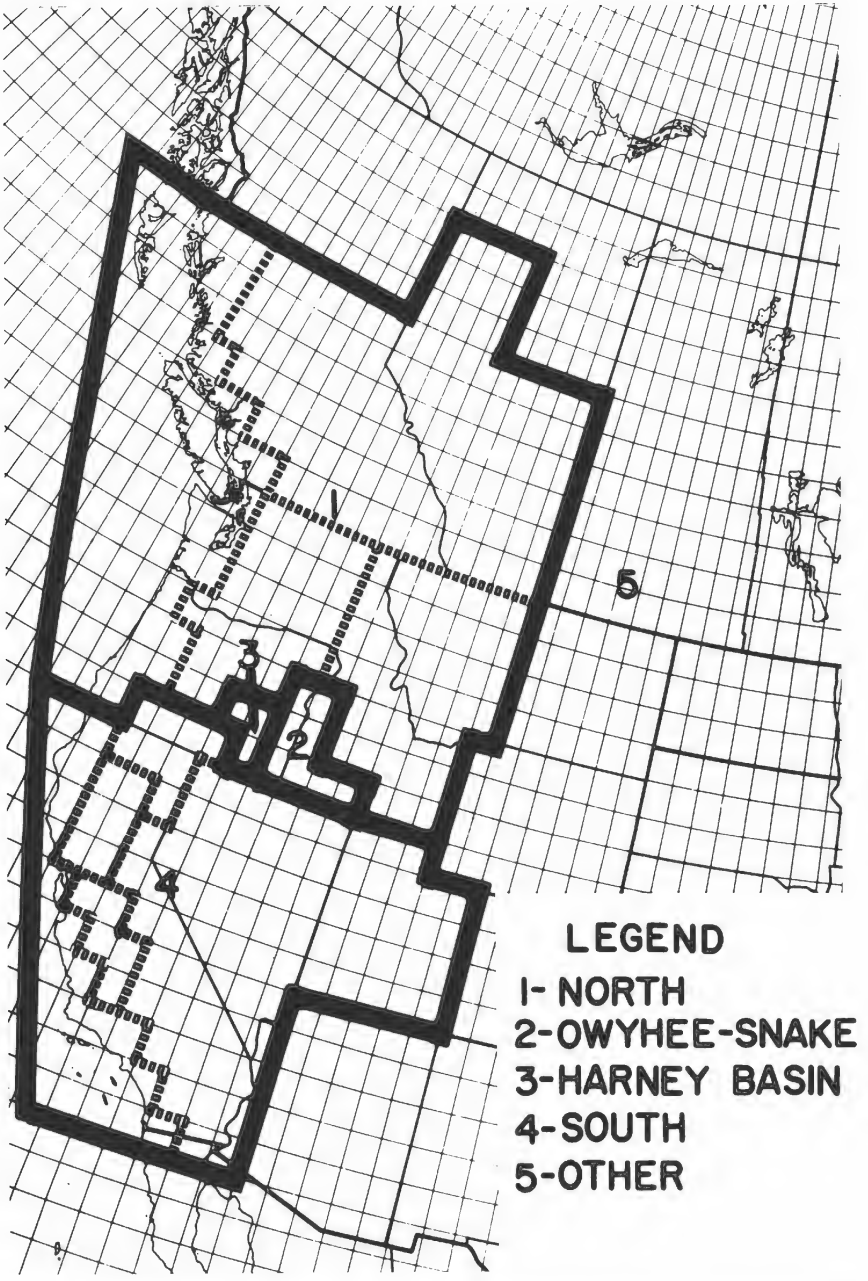

Figure 1. Reference areas (dashed lines) and reference units (solid lines) of recoveries of mallards banded at Malheur National Wildlife Refuge. Malheur National Wildlife Refuge is located in reference unit 3.

TABLE 1. Geographic distribution of indirect recoveries of female mallards banded at Malheur National Wildlife Refuge. Recoveries expressed as percent.

Season of Banding Decade of Recovery	N	Reference Unit of Recovery North of Harney Basin	Owyhee-Snake	Harney Basin	South of Harney Basin	Other	Total
Preseason							
1930-39	35	16.7	25.0	2.8	52.8	2.8	100.1
1940-49	120	6.7	23.3	4.2	65.0	0.8	100.0
1961-71	183	10.4	8.2	8.2	72.7	0.5	100.0
Spring							
1930-39	111	28.8	22.5	2.7	37.8	8.1	99.9
1940-49	49	8.2	30.6	6.1	55.1	0	100.0
1961-71	35	20.0	20.0	8.6	51.4	0	100.0
Inseason							
1930-39	260	38.1	11.2	6.2	43.1	1.5	100.1
1940-49	140	27.1	22.1	5.7	43.6	1.4	99.9
Postseason							
1961-71	42	47.6	7.1	31.0	11.9	2.4	100.0

TABLE 2. Geographic distribution of indirect recoveries of male mallards banded at Malheur National Wildlife Refuge. Recoveries expressed as percent.

Season of Banding Decade of Recovery	N	Reference Unit of Recovery North of Harney Basin	Owyhee-Snake	Harney Basin	South of Harney Basin	Other	Total
Preseason							
1930-39	62	22.5	16.1	1.6	59.6	0	99.8
1940-49	154	13.5	16.2	2.6	63.7	3.9	99.7
1961-71	339	12.7	10.6	5.6	70.5	0.6	100.0
Spring							
1930-39	151	29.1	21.9	4.6	40.4	4.0	100.0
1940-49	117	17.9	14.5	1.7	64.9	0.9	99.9
1961-71	121	21.5	9.9	6.6	61.2	1.1	100.3
Inseason							
1930-39	282	21.6	17.4	6.4	52.1	2.5	100.0
1940-49	366	18.8	17.8	8.5	52.7	2.2	100.0
Postseason							
1961-71	187	25.1	17.1	28.9	27.8	1.1	99.9

TABLE 3. Chi-square values from tests of geographic distributions of indirect recoveries among season of banding within decade of recovery. Only recovery distributions with greater than 75 recoveries were tested.

Banding Season	Recovery Decade	Sex	X^2 Value	Degrees of Freedom
Preseason and Spring	1940s	M	6.19	11
Preseason and Spring	1960s	M	13.04	11
Preseason and Inseason	1940s	M	23.01*	11
Preseason and Inseason	1940s	F	30.84*	11
Preseason and Postseason	1960s	M	115.43*	11
Spring and Inseason	1930s	F	29.93*	11
Spring and Inseason	1930s	M	23.06*	11
Spring and Inseason	1940s	M	19.09	11

*Significant at the 5 percent level.

spring, nearly half or more of the recoveries of each sample recorded as occurring south of the Harney Basin occurred in a 6-degree-block area comprising the Sacramento Valley, California (Table 5). Of the mallards banded postseason (and recovered in 1961-

1971) and recovered north of the Harney Basin, nearly 75 percent were recovered along the Columbia River in Oregon and Washington.

Because of small sample sizes ($n < 75$), many comparisons of geographic distribution of indirect recoveries among decades of recovery (and within season of banding) could not be tested statistically (Tables 1 and 2). Of the possible comparisons tested, only males banded in spring had significantly different recovery distributions between the 1930s and 1940s ($X^2 = 22.3$; $df = 11$) and between the 1930s and 1960s ($X^2 = 26.2$; $df = 11$).

TABLE 4. Geographic distribution of direct recoveries of mallards banded preseason from 1960-1971. Recoveries expressed as percent.

		Reference Area of Recovery					
Sex and Age	N	North of Harney Basin	Owyhee-Snake	Harney Basin	South of Harney Basin	Other	Total
Male							
Adult	96	10.4	9.4	3.1	77.1	0.0	100.0
Immature	174	7.5	14.9	24.7	52.3	0.6	100.0
Female							
Adult	91	5.5	9.9	7.7	76.9	0.0	100.0
Immature	111	2.7	11.7	17.1	68.5	0.0	100.0

TABLE 5. Percent of indirect recoveries of mallards banded in the Harney Basin that were recovered in the Sacramento Valley, California.

	Recoveries of Mallards in the Sacramento Valley as:			
Season of Banding	Percent of Total Indirect Recoveries		Percent of Indirect Recoveries from South of Harney Basin	
Decade of Recovery	Male	Female	Male	Female
Preseason				
1930s	29.0	36.1	48.6	68.4
1940s	42.4	44.2	66.3	67.8
1960s	46.9	47.8	66.5	66.2
Spring				
1930s	24.5	23.4	60.7	61.9
1940s	41.8	28.6	64.5	51.9
1960s	43.0	42.9	70.3	83.3

Nonetheless, the indirect recovery distribution changed from the 1930s to the 1960s (Tables 1 and 2). The transient population unit (banded preseason and in spring) displayed a consistent trend toward an increased concentration of recoveries in areas south of Harney Basin. Most of this change occurred because of an increased rate of recovery in the Sacramento Valley. Most of the rest of the reference areas located south of Malheur NWR had only minor changes in rate of indirect recovery except for the Klamath Basin-Warner Valley (N.E. California-S. Oregon) reference area which had nearly a 50 percent decrease in the rate of indirect recovery.

Recovery distributions reflect distribution and success of hunters, band reporting rates, and distribution of mallards. Sale of duck stamps increased at approximately the same rates in California and Oregon between 1934 and 1971 (Martin and Carney, in prep.). Thus, most of the change in recovery distribution cannot be attributed to changes in hunter distribution. We have no readily available data to measure changes in distribution of mallards, intensity of hunting, or success of hunters.

Chronologic Distribution of Recoveries

Analysis of chronologic distribution of indirect recoveries did not reveal nearly as distinct patterns as did geographic distribution of the same recoveries (Fig. 2). Differences between chronologic distribution of indirect recoveries of males and females within season of banding and decade of recovery were insignificant, and thus we combined indirect recovery distributions of males and females. In the 1930s, indirect recoveries of mallards banded inseason occurred significantly later than indirect recoveries of mallards banded preseason and of mallards banded in spring (Table 6). In the 1940s recovery decade, indirect recoveries of mallards banded inseason were nearly evenly distributed over a 12-week period from mid-October to early January, while indirect recoveries of mallards banded preseason were concentrated in mid-October, December, and early January; the difference was significant. Although several other significant chronologic distributions of indirect recoveries occurred, no clear patterns emerged.

Several patterns were noted among decades of recovery within season of banding (Fig. 2). Recoveries in the 1930s were concentrated between mid-October and early

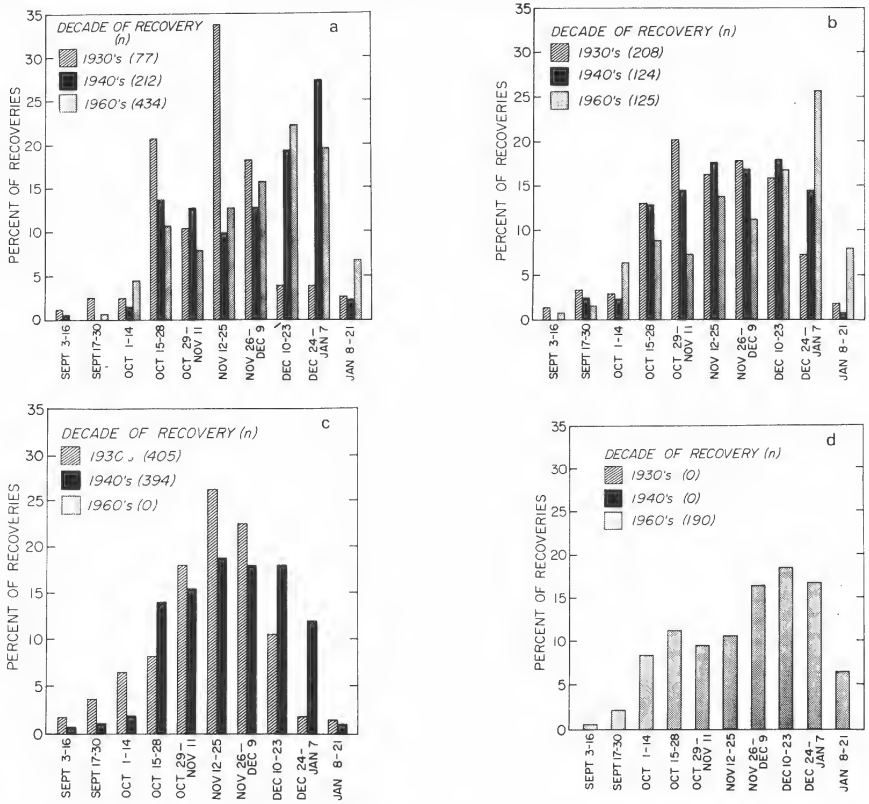

Figure 2. Chronologic distribution of indirect recoveries of male and female mallards banded at Malheur National Wildlife Refuge preseason (a), spring (b), inseason (c), and postseason (d).

December and reflected the short hunting seasons prevalent during the 1930s. Recoveries in the 1940s and 1960s displayed a bimodal pattern with a minor peak of recoveries in mid- to late October and a major peak in December and early January. This pattern was most prominent in the transient population (preseason and spring) and weak (inseason) or nonexistent (postseason) in the wintering population. The second and major peak in recoveries of the transient population probably corresponded with the arrival of mallards from this population in the Sacramento Valley.

TABLE 6. Chi-square values of tests of chronologic distributions among seasons of banding in the same decade of recovery of male and female mallards banded at Malheur National Wildlife Refuge.

Banding Seasons	Recovery Decade	X^2 Value	Degrees of Freedom
Preseason and Spring	1930s	21.06*	9
Preseason and Spring	1940s	17.95*	9
Preseason and Spring	1960s	10.38	9
Preseason and Inseason	1930s	20.98*	9
Preseason and Inseason	1940s	32.63*	9
Preseason and Postseason	1960s	10.88	9
Spring and Inseason	1930s	29.21*	9
Spring and Inseason	1940s	3.15	9
Spring and Postseason	1960s	6.70	9

*Significant at the 5 percent level.

The distribution of direct recoveries of mallards banded preseason and recovered in the 1960s indicated that immatures were recovered earlier than adults (Fig. 3). However, only the difference between adult and immature males was significant. As for indirect recoveries, there were no significant differences between chronological distributions of direct recoveries of males and females within ages.

Survival and Recovery Rates

Survival and recovery rates were estimated only for mallards banded preseason from 1960 to 1971. Age determination of mallards banded prior to 1950 appeared to have

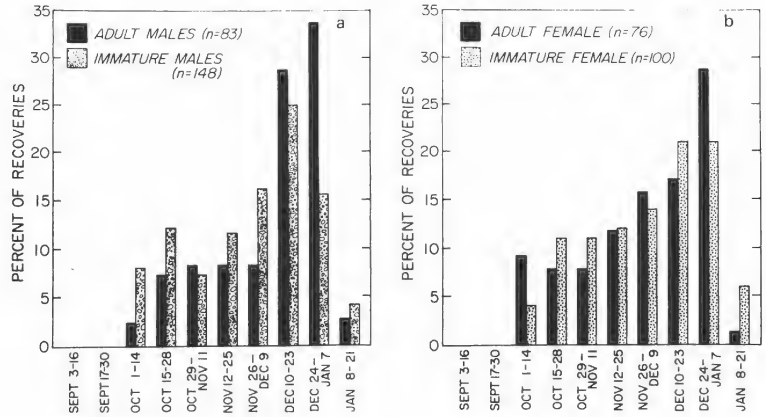

Figure 3. Chronologic distribution of direct recoveries of male (a) and female (b) mallards banded preseason, 1960-1971, at Malheur National Wildlife Refuge.

been inaccurate and hence those samples were excluded from anaylsis. The remaining banded samples were too small to warrant analysis.

Chi-square goodness of fit tests indicated that the data for males ($X^2 = 41.0$; df = 37) and females ($X^2 = 26.3$; df = 22) fit model H_1 of Brownie (1973) and Brownie and Robson (1974). Immature males had significantly lower survival rates (0.377; Table 7) than all other age and sex classes (Table 8); immature males also had the

TABLE 7. Estimates of average annual survival rates and average annual recovery rates for mallards banded preseason in the Harney Basin, and recovered from 1960-1971.

Age	Sex	Survival Rate ±SE	Recovery Rate ±SE
Adult	Male	0.628 ± 0.035	0.071 ± 0.006
Immature	Male	0.377 ± 0.046	0.085 ± 0.008
Adult	Female	0.586 ± 0.081	0.061 ± 0.007
Immature	Female	0.569 ± 0.105	0.063 ± 0.007

TABLE 8. Z-values from tests of recovery rates and tests of survival rates between different sex and age classes of mallards banded preseason and recovered from 1960-1971.

Sex and Age Classes Tested	Z-value for Survival Rates	Z-value for Recovery Rates
Adult male and Immature male	4.53**	1.48
Adult female and Immature female	0.12	0.20
Adult male and Adult female	0.47	1.01
Immature male and Immature female	1.68*	2.12**

*Significant at the 10 percent level.
**Significant at the 5 percent level.

highest recovery rates (0.085). Apparently the low survival of immature males resulted from their high vulnerability to hunting. The recovery rate and survival rate of immature females (0.063 and 0.569, respectively) were not significantly different from those of adult females (0.061 and 0.586, respectively). Females, both adult and immature, had lower survival rates and lower recovery rates than adult males (0.628 and 0.071, respectively); the differences were not significant. Recovery rates provide a direct index to hunting mortality. The lower recovery and survival rates for females than for males indicates that survival of females was less dependent on hunting than was survival of males. These differences were particularly evident for immature males and females.

Discussion

The wintering population at Malheur NWR (banded inseason and postseason) appeared to be a small segment of the mallard population that winters in the Columbia-Snake River Basin (Eastern Washington, Northeastern Oregon, Southern Idaho). Average peak number of mallards present in winter at Malheur NWR from 1960 to 1971 was 4500 (Malheur NWR Files); mid-winter inventories of the mallard population in the Columbia-Snake River Basin (1960-1971) yielded an average count of 1.3 million (pers. comm., J. Chattin, Pacific Flyway Representative).

The transient population was probably composed of mallards breeding in the Harney Basin, and migrants that bred further north but moved south early enough to be

banded preseason. Average peak numbers of mallards present at Malheur NWR during migration (spring and fall) was 15,000 during 1960-1971 (Malheur NWR Files). Average number of mallards breeding at Malheur NWR from 1965-1971 was 2858; average estimated production from 1960-1971 was 2728. Most of these 5500 mallards that survived to migrate to wintering areas apparently were associated with the 0.5 million mallards in the Sacramento Valley (pers. comm., J. Chattin).

The average recruitment required for a stationary population with the survival rates of mallards banded preseason (and recovered in the 1960s) was 1.46 immatures produced per breeding female (Henny *et al.*, 1970:694; Formula 9). The estimated average number of mallards raised to flight stage per breeding female mallard during 1966-71 was 1.57 (Malheur NWR Files). Thus the population should have been increasing slightly or remained constant, and from 1965 to 1971 there was no detectable change in the number of pairs of mallards present in spring (Malheur NWR Files).

Anderson and Henny (1972) analyzed the geographic and chronologic distribution of recoveries of mallards banded preseason in North America between 1950 and 1970. We noted several discrepancies between distribution of mallards banded in their Eastern Oregon minor reference area (which included Malheur NWR) and those banded preseason at Malheur NWR from 1961 to 1970 (few mallards were banded at Malheur NWR in the 1950s).

In all cases (male and female, direct and indirect, and immature and adult), the distribution noted by Anderson and Henny (1972) displayed a greater proportion of recoveries in Oregon and a lower proportion in California than our analyses (Table 9).

TABLE 9. Recovery distributions of mallards banded preseason throughout Eastern Oregon (1950-1969) and at Malheur NWR (1961-1971). Recoveries expressed as a percent. Recovery distribution of mallards banded throughout Eastern Oregon from Anderson and Henny (1972).

	Direct				Indirect	
	Juveniles		Adult		Total	
Sex Recovery Area	Eastern Oregon	Malheur NWR	Eastern Oregon	Malheur NWR	Eastern Oregon	Malheur NWR
Male						
Washington	0.3	0.5	1.5	2.1	3.9	2.6
Oregon	80.2	34.5	60.1	10.4	25.5	16.7
Idaho	2.8	14.9	1.5	9.4	6.1	9.7
California	16.0	47.7	35.5	71.9	56.7	61.3
Other	0.6	2.1	1.5	6.3	8.0	9.7
N	706	174	341	96	593	341
Female						
Washington	1.5	0.9	0.5	0	3.9	3.4
Oregon	78.5	27.9	65.8	17.6	36.0	17.6
Idaho	1.2	6.3	3.2	7.7	5.0	7.4
California	17.6	61.3	29.7	72.5	49.2	68.8
Other	1.2	3.9	0.9	2.2	5.9	2.9
N	409	111	219	91	258	176

Similarly, their chronologic distribution showed a greater proportion of recoveries in October and a lower proportion in December and January than our analyses (Figures 2 and 3). Apparently, mallards of the transient population at Malheur NWR were a distinct subunit of the mallard population that occurred in Eastern Oregon in late summer and early fall.

Several estimates of survival of mallards in the western portion of the Pacific Flyway

were made in the past using deterministic models (life tables) (Geis *et al.*, 1969, Hickey, 1952). Our estimates of survival were derived from stochastic models and hence are not directly comparable to the earlier estimates. Life tables require unrealistic and restrictive assumptions for estimation of survival rates from band recovery data, and provide unreliable estimates of survival (Anderson, 1972, 1975; Cormack, 1968, 1972; Seber, 1972, 1973; Taylor 1966).

Recently Anderson (1975) estimated survival and recovery rates of mallards in North America using the same stochastic model we employed. The continent-wide average survival of adults was similar to the survival rates of adults from Malheur NWR. Survival rates of immature mallards from Malheur NWR were much lower for immature males (0.377 vs 0.480), and much higher for immature females (0.569 vs 0.460), than the continent-wide average for immature males and immature females, respectively. Survival rates of adult male, adult female, and immature female mallards from all of Eastern Oregon (Anderson, 1975:52 and 76) were similar to survival rates of the same age and sex classes of mallards banded preseason at Mallheur NWR; immature males from Malheur NWR survived at a much lower rate than immature males from all of Eastern Oregon (0.377 vs 0.508).

Recovery rates of immatures from all of Eastern Oregon were approximately twice recovery rates of immatures banded preseason at Malheur NWR (Anderson 1975:52 and 76). The low recovery rates of immature mallards from Malheur NWR may be due to low band reporting rates. Band reporting rates are usually low within 80 miles of the banding station (Henny and Burnham, 1975), and immature mallards banded at Malheur NWR tended to be recovered predominantly in the Harney Basin early in the season. Recovery rates for adults were similar for mallards banded at Malheur NWR (Table 7) and in all of Eastern Oregon (Anderson, 1975:52).

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Literature Cited

Anderson, D. R. 1972. Bibliography on Methods of Analyzing Bird Banding Data with Special Reference to the Estimation of Population Size and Survival. U.S. Fish and Wildl. Serv., Spec. Sci. Rep., Wildl. 156. 13 pp.

————. 1975. Population Ecology of the Mallard: V. Temporal and geographic estimates of survival, recovery, and harvest rates. U.S. Fish and Wildl. Serv., Resource Publ. 125. 110 pp.

————, and C. J. Henny. 1972. Population Ecology of the Mallard: I. A review of previous studies and the distribution and migration from breeding areas. U.S. Fish and Wildl. Serv., Resource Publ. 105. 166 pp.

Brimlow, G. F. 1951. Harney County, Oregon, and Its Rangeland. Binfords & Mort, Portland, Or. 316 pp.

Brownie, C. 1973. Stochastic Models Allowing Age-Dependent Survival Rates for Banding Experiments on Exploited Bird Populations. Cornell Univ., Ithaca, New York. Ph.D. Thesis. 114 pp.

————, and D. S. Robson. 1974. Models Allowing for Age-Dependent Survival Rates for Band-Return Data. Biometrics Unit, Cornell University, Ithaca, New York BU-514-M. 27 pp.

Cormack, R. M. 1968. The statistics of capture-recapture methods. Oceanogr. Mar. Biol. Ann. Rev. 6:455-506.

————. 1972. The logic of capture-recapture estimates. Biometrics 28:337-343.

Erickson, R. C. 1948. Life history and ecology of the canvasback (*Nyroca valisneria,* Wilson) in southeastern Oregon. Iowa State Coll. J. Sci. 23:30-32.
Geis, A. D., R. K. Martinson, and D. R. Anderson. 1969. Establishing hunting regulations and allowable harvest of mallards in the United States. J. Wildl. Manage. 33:848-859.
Henny, C. J., and K. P. Burnham. 1975. A reward band study of mallards to estimate band reporting rates. J. Wildl. Manage. 40:1-14.
————, W. S. Overton, and H. M. Wight. 1970. Determining parameters for populations using structural models. J. Wildl. Manage. 34:690-703.
Hickey, J. J. 1952. Survival Studies of Banded Birds. U.S. Fish and Wildl. Serv., Spec. Sci. Rep., Wildl. 15. 177 pp.
Jarvis, R. L., and S. W. Harris. 1967. Canada goose nest success and habitat use at Malheur Refuge. Murrelet 48:46-51.
————, and ————. 1971. Land-use patterns and duck production at Malheur National Wildlife Refuge. J. Wildl. Manage. 35:767-773.
Martin, E. M. and S. M. Carney (in preparation). Population Ecology of the Mallard: IV. A review of duck hunting regulations, activity and success, with special reference to the mallard. U.S. Fish and Wildl. Serv., Resource Publ.
Robson D. S., and C. Brownie. 1973. Estimation of Annual Mortality Rates from Waterfowl Banding Records. Biometrics Unit, Cornell Univ. Ithaca, New York. BU-444-M. 82 pp.
Seber, G. A. F. 1972. Estimating survival rates from bird-banding returns. J. Wildl. Manage. 36: 405-413.
————. 1973. The Estimation of Animal Abundance and Related Parameters. Charles Griffin and Co. Ltd., London. 506 pp.
Sooter, C. A. 1938. Waterfowl Nesting Studies on Malheur Migratory Bird Refuge, Oregon, in 1938. 32 pp. Mimeogr.
————. 1940. Progress Report: Duck Nesting Studies on Malheur National Wildlife Refuge in 1939 and 1940. 48 pp. Mimeogr.
Taylor, S. M. 1966. Recent quantitative work on British bird populations. The Statistician 16:119-170.

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The Vertical Distribution of Needles and Branchwood in Thinned and Unthinned 80-Year-Old Lodgepole Pine

Abstract

About 30 years after thinning part of a 50-year-old stand, trees in adjacent thinned and unthinned lodgepole pine in southern Wyoming were studied to compare relative dry matter production of needles and branches and the distribution of their weights. The weight distribution within the canopy of the study trees was determined using a Weibull probability density function. In the thinned part of the stand, the observed and theoretical weight distribution of both needles and branchwood was symmetrical and much like a normally distributed population. In the unthinned part of the stand, weight distribution of needles and branchwood was strongly skewed upward in the top half of the canopy. The strong upward displacement of needles and branchwood was interpreted as further evidence of growth stagnation in the unthinned area.

Introduction

Lodgepole pine (*Pinus contorta* Dougl.) frequently regenerates too abundantly, and growth stagnates after a few years. The resulting single-storied, dense "dog-hair" stands (up to 100,000 or more trees per ha) can stay alive for as long as a 100 years, but make little height or diameter growth. Trees 50 to 60 years old have an average height often less than 2 m and a diameter less than 3 cm. Early heavy thinning is necessary to obtain satisfactory diameter and height growth in such stands (Alexander, 1956; Barrett, 1961).

Adjacent areas of thinned and unthinned lodgepole pine, located about 3.4 km southeast of Foxpark in southern Wyoming, afforded the opportunity to compare relative dry matter production of branches and needles and the distribution of their weights within the respective canopies. Information about the characteristics of lodgepole pine crowns is generally lacking. When more is known about the crowns, it should be possible to develop good models of canopy biomass distribution. In other timber types, such models have provided a useful tool to study the interaction among physical factors and physiological processes of growth, and also to interpret changes over time and thus provide possible management options (Schreuder and Swank, 1974).

Study Area

The study was conducted in an extensive 80-year-old lodgepole pine forest that resulted from natural reseeding on a burned-over area. The area was about 2470 m in elevation, and the terrain was relatively flat. When the trees were about 50 years old, a portion of the stand was thinned in 1939-40 by the Civilian Conservation Corps. Tree growth in the area is generally slow, and because of low economic value, the initial thinning was done with no plan for further thinning (Woodhead, 1934).

In 1970, few trees had died in the thinned area. Spacing averaged about 2.3 m or about 2000 trees per ha. Average height of trees was 10.7 m. Diameter at breast height

(d.b.h.) for some 2500 trees in the thinned area ranged from 3.6 to 25.7 cm and averaged 12.8 cm. Basal area of the trees was about 28m^2/ha (125 ft^2/acre). The adjacent unthinned part of the forest, less than 60 m away, based on three 10 m^2 plots averaged between 25,000 and 50,000 trees/ha. Average height of the trees was about 7.6 m. Diameters ranged from 1 to 8 cm and average diameter was 3.1 cm. Basal area in the unthinned part of the stand was about 34 m^2/ha (149 ft^2/acre).

Measurements

Crown biomass relations and comparisons were determined in 1970 for five randomly selected trees taken from the thinned area. The trees were among a group of about 100 trees removed to make a 10 x 50 opening which was used to determine the clearing effect upon airflow and snow accumulation (Bergen, 1975; Gary, 1974). Five additional trees, subjectively selected to represent the unthinned part of the stand, were also studied.

Field measurements on the 10 trees included d.b.h., height to first dead and live branches, height of each succeeding annual whorl, and tree height. All branches from the annual whorls were removed from each tree, tagged for identification and oven dried to obtain weights of needles and branchwood.

Results

Bole and Crown Dimensions

All trees in the thinned part of the stand were generally released from early growth stagnation. The relative differences between the thinned and unthinned areas as indicated by the sample trees are given in Table 1. Thirty years after the initial thinning, the

TABLE 1. Average bole and crown dimensions 30 years after thinning.

Variable	Stand Condition	
	Thinned	Unthinned
Diameter breast height (cm)	11.2±0.5[1]	5.6±1.17
Height to 1st dead whorls (m)	1.49±0.18	1.47±0.45
Height to all-live crown (m)	5.60±0.48	4.84±1.30
Crown length (m)	4.36±0.22	2.64±0.58
Tree height (m)	9.95±0.60	7.47±0.97
Crown length/height	.44	.36

[1]Standard deviation

largest difference between the two samples of trees was bole diameter. Diameters of trees from the unthinned area averaged 5.6 cm and 11.2 cm for trees from the thinned area. Average basal area for trees from the unthinned part of the stand was 25.9 cm^2. In contrast, trees from the thinned part had an average basal area of 98.3 cm^2 and were approximately 3.8 times larger.

The next largest difference between the two groups of trees was live crown length. As a result of the wider tree spacing, crown length in the thinned part of the stand was about 65 percent longer, and thus had greater photosynthetic potential for future growth (Madgwick, 1970). The relative difference in tree height was less than the difference in diameter and crown length.

Comparisons of the annual height or leader growth, however, indicated a decline of 28 percent during the last 20 years in both the thinned and unthinned portion of the stand (Table 2). It was not known whether the tapering off of growth for trees taken from the thinned part of the stand indicated another period of growth stagnation or whether normal height growth was merely slowing. Average annual terminal growth

during the last 20 years was 14.4 cm and 9.9 cm for trees on the thinned and unthinned areas, respectively. Based on cumulative annual terminal growth for 30 years since thinning, height growth was 25 percent greater on trees in the thinned area than those in the unthinned area.

TABLE 2. Average annual decline in leader growth (cm).

Leader	Stand Condition	
age (years)	Thinned	Unthinned
16-20	16.7±7.3[1]	11.8±3.6
11-15	15.6±7.5	10.4±2.9
6-10	13.2±7.1	8.9±3.2
0-5	12.0±4.9	8.5±2.7

[1]Standard deviation

Branch Development and Dry Matter Production

In lodgepole pine, as in many other conifers, the larger branches generally arise from auxiliary buds at the apex of the leader, while the smaller branches develop from latent buds along the leader. Both types of branches collectively formed the annual whorl of branches, and their ages could be counted fairly accurately up to 20 years. Number of live branches per whorl, over the most recent 20-year period, averaged 3.6 for trees in the thinned area and 3.5 in the unthinned area, ranging from one to eight in both groups of trees.

Mean diameter computed for the largest branch from 20-year-old whorls was 14.4 mm for trees in the thinned area and 9.1 mm for trees in the unthinned area. Mean diameter of the largest 1-year-old branches was 5.6 mm for trees in the thinned area and 7.5 mm, or slightly larger, for study trees in the unthinned area.

Mean lengths computed for the longest branch on 20-year-old annual whorls was 90.6 cm for trees in the thinned area and 46.5 cm, or about one-half as long, for trees in the unthinned area. Mean length for the longest 1-year-old annual whorl branches ranged from 15.0 cm to 10.5 cm for trees in the thinned and unthinned areas, respectively.

The initial development of all branch whorls was apparently similar, but branch size varied greatly over time due to yearly variation in the growing season, continual changes in the crown environment, and factors of competition. During the past 20 years (between 10 and 30 years after initial thinning) the cumulative weight of branchwood in the annual whorls of trees growing in the thinned area reached about 1.1 kg per tree or about 5.4 times more than their counterparts in the unthinned area (Fig. 1). For trees in the thinned area, there was a definite, although inconsistent, trend of increase in weight of the annual growth. Weight changes were negligible for branches older than about 8 or 9 years for trees in the unthinned part of the stand.

The cumulative production of needles was considerably greater than production of branchwood. If cast needles could have been accounted for, the ratios of needles to branchwood weights computed below would have been considerably greater:

	Needle/branchwood Weight
Thinned area	1.50
Unthinned area	2.36

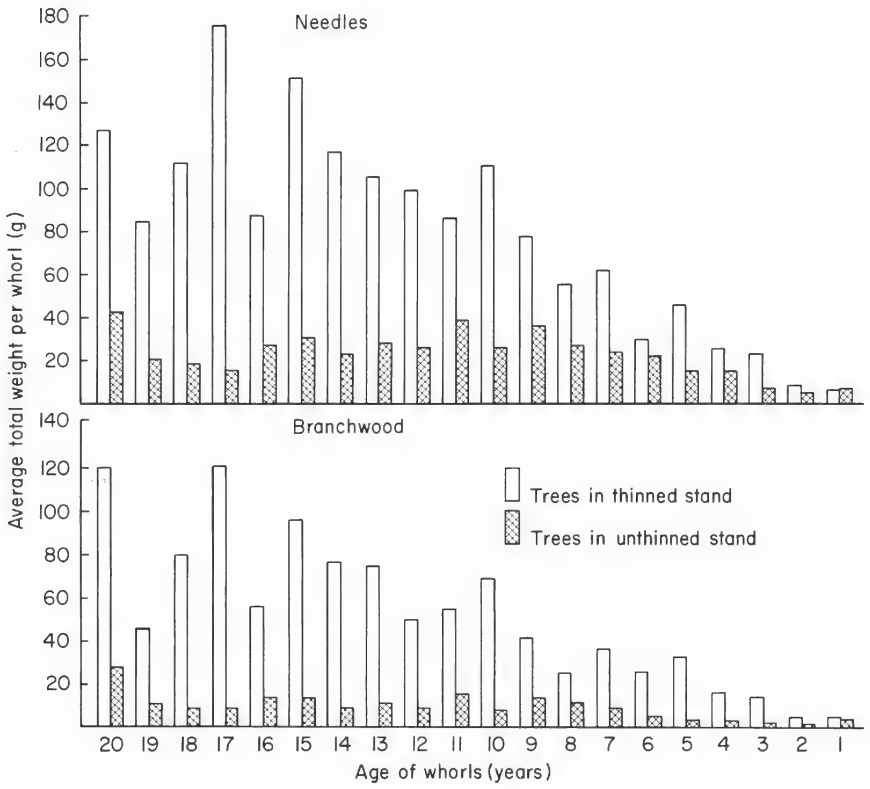

Figure 1. Average ovendry weights of needles and branchwood by age of whorls.

The correlation coefficient between weights of needles and branchwood was 0.96 for trees in the thinned area and 0.88 in the unthinned area.

Vertical Distribution of Needles and Branchwood

Individual tree crowns in both stand densities had wide gaps, both horizontally and vertically, between the needles and branches of successive whorls. Similar characteristics were observed by Stiell (1962) and apparently are common to all conifers. Because of the wide variability of tree heights, crown lengths, and amounts and location of needles and branchwood, analysis of individual tree crowns yielded little information about the relative distribution of needles and branches within the canopy itself.

Since the canopy is usually of greater interest from the standpoint of energy budgets, nutrients fluxes, etc., the distributions of needles and branches were computed in terms of canopy. For this purpose, the crowns of the five study trees in each area were assumed to represent collectively the stand canopy. The limits of the two canopies en-

compassed the space from the tip of the tallest tree down to the level of the lowest all-live whorl, usually on a different tree. The upper level of the canopy was about 1.5 m

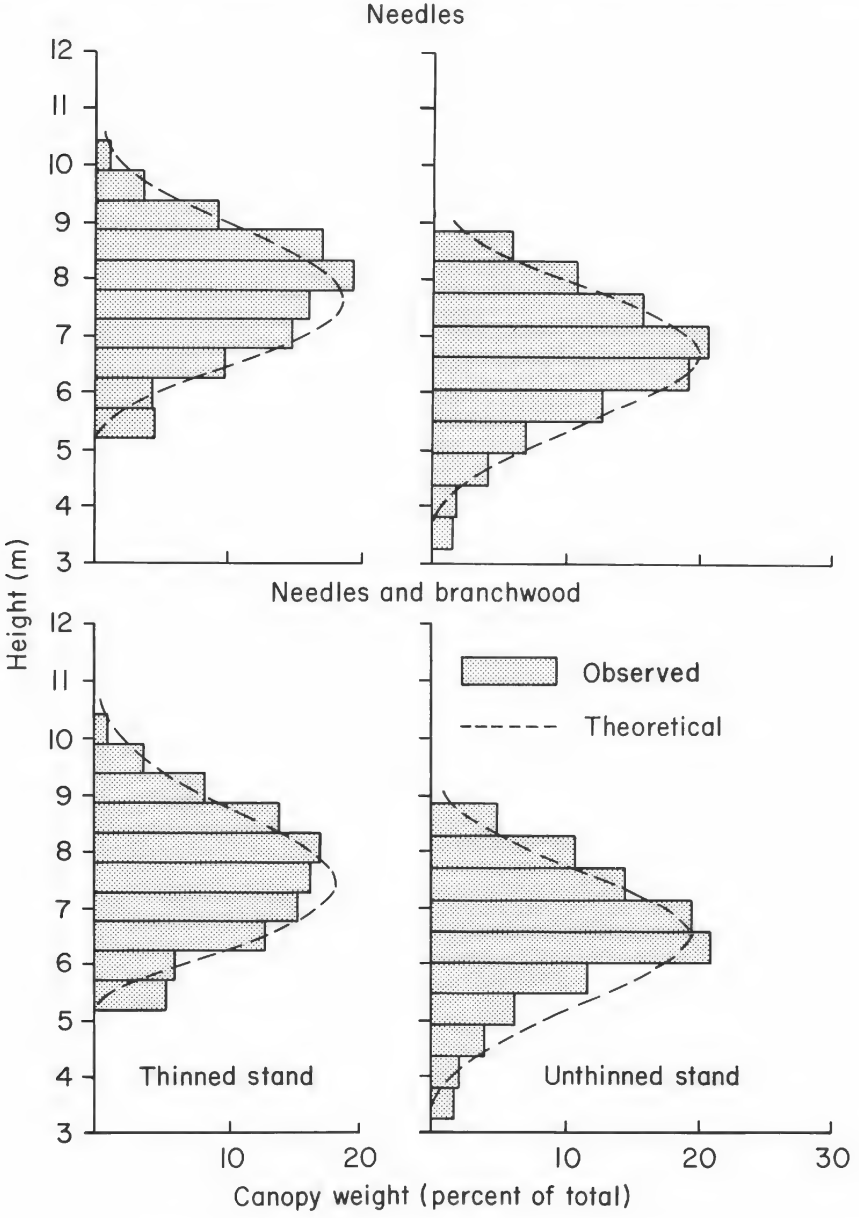

Figure 2. Vertical weight distribution of needles and needles plus branchwood for 10 equal height sections within the canopy space.

higher in the thinned area, while canopy depth was about 0.5 m less than in the unthinned area.

A Weibull probability density function was fitted to characterize vertical weight distribution of needles and branchwood within the assumed canopies. This model has gained wide acceptance for characterizing diameter distributions (Bailey and Dell, 1973) and appears equally versatile for determining foliage weight distribution (Schreuder and Swank, 1974).

For grouping the weight parameters, it was assumed that all main and internodal branches within an individual whorl were attached to the bole at the same relative height. It was further assumed that all branches grew horizontally and did not overlap the next higher whorl. Figure 2 shows the computed vertical weight distribution (proportion of total weight of needles and needles plus branchwood) for 10 equal height sections within the canopy space.

The Weibull model gave a good characterization of the distribution of needles and needles plus branchwood weights. The distribution of needles within the thinned part of the stand was nearly symmetrical and very much like a normally distributed population, with about 50 percent of the needle weight in both the lower and upper halves of the canopy. In contrast, about 75 percent of the needle weight for trees in the unthinned part of the stand was skewed upward and located in the upper half of the canopy space. The weight distribution of needles plus branchwood exhibited about the same patterns as that shown for needles, although in both areas the midpoint of weight distribution of needles plus branchwood was skewed slightly downward due to larger branches in the lower half of the canopy.

Summary and Conclusion

Organic matter production is generally proportional to leaf mass. Where site conditions and climate allow a stand to close, organic production will generally reach a constant level or a balance between developing and dying needle and branch tissue (Tadaki, 1966). The nearly symmetrical distribution of needle mass within the canopy in the thinned area apparently indicated the stand canopy was closed or nearly so. Thus, on the basis of needle distribution, it was concluded that organic production was near a constant level for the present stand density. In the unthinned part of the stand, about 75 percent of the needle and branchwood mass was in the upper half of the canopy space. This distribution pattern indicated obvious stand closure and a pattern of general decadence of branch tissue and needle production for the lower half of the canopy.

Thirty years after thinning, breast height diameters of trees in the thinned part of the stand averaged about twice as large—or nearly four times larger in basal area. Height growth was 25 percent greater in the thinned area, and the trees had grown to marketable small pole sizes. Few trees in the unthinned part of the stand will ever grow to pole size.

Literature Cited

Alexander, R. R. 1956. Two methods of thinning lodgepole pine in the central Rocky Mountains. J. For. 54:99-102.

Bailey, Robert L., and T. R. Dell. 1973. Quantifying diameter distributions with the Weibull function. For. Sci. 19:97-104.

Barrett, James W. 1961. Response of 55-year-old Lodgepole Pine to Thinning. U.S. Dept. Agric., For. Serv. Pac. Northwest For. and Range Exp. Stn., Res. Note 206. 8 pp.

Bergen, J. D. 1975. Air movement in a forest clearing as indicated by smoke drift. Agric. Meteorol. 15:165-179.
Gary, Howard L. 1974. Snow accumulation and snowmelt as influenced by a small clearing in a lodgepole pine forest. Water Resour. Res. 10:348-353.
Madgwick, H. A. I. 1970. Biomass and productivity models of forest canopies. Pp. 47-54 *In* Analysis of Temperate Forest Ecosystems. D. E. Reichle (Ed.), Springer-Verlag, New York. 304 pp.
Schreuder, Hans T., and Wayne T. Swank. 1974. Coniferous stands characterized with the Weibull distribution Can. J. For. Res. 4:518-523.
Stiell, W. M. 1962. Crown Structure in Plantation Red Pine. Can. Dep. For., For. Res. Branch Tech. Note 122, 36 pp.
Tadaki, Yoshiya. 1966. Some discussions on the leaf biomass of forest stands and trees. Bull. Gov. For. Exp. Stn. 184-135-161. Tokyo, Japan.
Woodhead, P. V. 1934. Thinning lodgepole pine stands in the central Rocky Mountain region. J. For. 32:594-597.

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Bryophyte Communities of Central Idaho Forests[1]

Abstract

Four bryophyte groups dominated by *Aulacomnium palustre*, *Brachythecium velutinum*, *Brachythecium collinum*, and *Tortula ruralis* characterize cryptogamic communities of coniferous forests in east-central Idaho. Within these four groups, five bryophyte associations are correlated with communities in a habitat type classification based on vascular plants. In the *Aulacomnium palustre* group, the *Aulacomnium palustre-Bryum weigelii* association found around seeps and springs occurs only in the *Abies lasiocarpa/Caltha biflora* habitat type; another hydric association, *Aulacomnium palustre-Amblystegium juratzkanum*, is restricted to the *Picea engelmannii/Carex disperma* habitat type; additionally, the *Aulacomnium palustre-Brachythecium velutinum* association occurs in the *Abies lasiocarpa/Calamagrostis canadensis* habitat type. Within the *Brachythecium velutinum* group, the only defined association, *Brachythecium velutinum-Polytrichadelphus lyallii*, occurs in the relatively mesic *Abies lasiocarpa/Vaccinium scoparium* habitat type. The *Brachythecium collinum* group and its one recognized association, *Brachythecium collinum-Dicranoweisia crispula*, occur throughout many different xeric habitat types. The *Tortula ruralis* group, for which no associations were defined, was found in the xeric *Pseudotsuga menziesii/Festuca idahoensis* habitat type.

Introduction

In the Pacific Northwest, we know relatively little about the ecological role of mosses in forest ecosystems. In British Columbia, Krajina (1965) used the dominant mosses to further subdivide forest vegetation into ecological units. Franklin and Dyrness (1973) included bryophytes in their vegetative descriptions of Oregon and Washington. However, many studies of forest ecosystems in the Pacific Northwest (Spilsbury and Smith, 1947; Becking, 1954; Daubenmire and Daubenmire, 1968; Pfister *et al.*, 1977; and Steele *et al.*, Habitat types of central Idaho, review draft, Intermountain Forest and Range Experiment Station, Ogden, Utah) have omitted the cryptogamic flora from the analyses and classification.

Obviously, cryptogams are part of the phytocoenosis; in order to determine their ecological role in forest habitats, the individual species must first be identified and the various combinations of species should then be classified and correlated with vascular plant communities. Results from a few studies in North America (Cooke, 1955; Looman, 1964; Hoffman and Kazmierski, 1969; Stringer and Stringer, 1974) indicate that cryptogams may be more sensitive to microclimate variations than the vascular flora. This finding suggests that cryptogams might be useful in classifying forest communities.

In the Northern Rocky Mountains the concept of habitat types (Daubenmire and Daubenmire, 1968) has provided a system for classifying forest lands according to the climax plant community that may develop on a site. In eastern Washington and northern Idaho, bryophytes were studied (Betty and Noe Higinbotham, Washington State University, Pullman, Washington) in conjunction with the Daubenmires' (1968) habitat type

[1]This article is based on a Master of Science thesis submitted to the University of Idaho in 1974. The Intermountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, provided financial support and assistance in identifying vascular plants and classifying sites. Elva Lawton, author of Moss Flora of the Pacific Northwest, assisted with some moss identifications.

classification. However, no other attempts have been made to correlate bryophyte communities with vascular plant communities in Idaho.

Recently, the Forest Service began extending the habitat type classification system into central Idaho. Working under a cooperative agreement with the Forest Service, I have described and classified moss communities in central Idaho and correlated these communities with forest habitat types. This study also attempts to determine the successional status of bryophytes within vascular communities and to evaluate their usefulness as ecological indicators.

Little information on bryophyte communities exists for central Idaho. A preliminary checklist of Idaho mosses (McCleary and Green, 1971) derived mainly from Fay MacFadden's collections in the Boise National Forest is available. This incomplete checklist and Lawton's (1971) *Moss Flora of the Pacific Northwest* provided the basic references for this study.

The study area includes the Sawtooth, Salmon, and Challis National Forests (Fig. 1). Study of the forest communities ranged from subalpine forests near upper timberline to lower timberline, which borders grasslands in the extreme north and sagebrush communities in the south. Within this elevational relief of 1524-2896 m (5000-9500 ft) *Pseudotsuga menziesii* var. *glauca* dominates at elevations between 1524-2134 m (5000 and 7000 ft) and often borders the grasslands and sagebrush communities. In other areas near lower timberline it mingles with *Pinus flexilis* or merges with a moun-

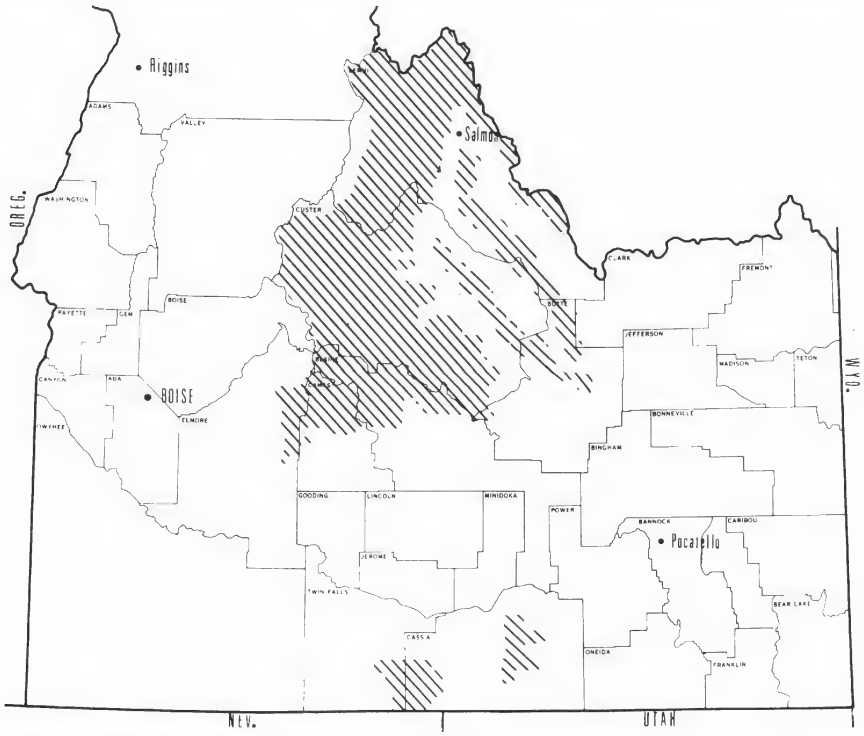

Figure 1. Primary study area (shaded) in central Idaho.

tain shrub community. At higher elevations of 2134-2896 m (7000-9500 ft) *Pinus contorta*, *Abies lasiocarpa*, and scattered *Picea engelmannii* characterize the forest types. Wind-deformed *Pinus albicaulis* mixed with stunted *Abies lasiocarpa* forms the upper timberline at about 3049 m (10,000 ft).

Mean annual precipitation in these forests ranges from 116 cm (45 in) in the subalpine forest of the Sawtooth Mountains to about 61 cm (24 in) at lower timberline near Challis (Soil Conservation Service, 1965).

Methods

Within the study area, I sampled 140 forest stands from May to August in 1973. Sample areas were chosen for their homogeneity in vegetation, and they were relatively free of major disturbances by fire, domestic grazing, and logging. The location of each sample area was recorded and is available (Steele, 1974). Sample plots were subjectively located on these sites to avoid rock outcrops, moist depressions, and other microsites atypical of the general bryophyte and vascular plant communities. In each stand a 375 m^2 circular plot set the limits of the macroplot. Within each macroplot I placed ten 2x1 dm microplots 4 dm apart along a transect from the center of the circle to the circle periphery. Direction of this transect was located subjectively for maximum uniformity in ground cover. Coverage estimates for each bryophyte species within the 2x1 dm microplot were recorded using the canopy cover technique described by Daubenmire (1959). These estimates were recorded as the following coverage classes: T=0-1 percent, 1=2-5 percent, 2=6-25 percent, 3=26-50 percent, 4=51-75 percent, 5=76-95 percent, 6=96-100 percent. Coverage was computed by taking the arithmetic average of the midpoint of the coverage classes as a measure of dominance within the bryophyte community. Frequency, the percentage occurrence of a species within the 10 microplots, and constancy, the percentage of occurrence of a species in sample stands of one association, were also calculated. These data were assembled in a synthesis table (Mueller-Dombois and Ellenberg, 1974) and stands were grouped according to their similarities in species composition. The final grouping of these stands illustrated five associations which were then named for the dominant moss members.

Sampling adequacy was evaluated using a species area curve (Daubenmire, 1959). Samples of each bryophyte were collected and later examined in the laboratory to verify field identifications. Voucher specimens were deposited in the University of Idaho Herbarium (ID).

Results

In the results, the term "association" refers to bryophyte communities having similar composition as well as dominant species. The collection of all associations and unclassified stands having the same dominant bryophyte was assigned to a group but not defined as an association.

Four bryophyte groups characterized by *Aulacomnium palustre*, (nomenclature follows Lawton, 1971), *Brachythecium velutinum*, *Brachythecium collinum*, and *Tortula ruralis* occurred in the study area. Further subdivision of some of these groups resulted in a total of five moss associations: *Aulacomnium palustre-Bryum weigelii*, *Aulacomnium palustre-Amblystegium juratzkanum*, *Aulacomnium palustre-Brachythecium velutinum*, *Brachythecium velutinum-Polytrichadelphus lyallii*, and *Brachythecium collinum-Dicranoweisia crispula*. The moss communities are classified as follows:

GROUPS ASSOCIATIONS

Aulacomnium palustre group
- Aulacomnium palustre-Bryum weigelii association
- Aulacomnium palustre-Amblystegium juratzkanum association
- Aulacomnium palustre-Brachythecium velutinum association

Brachythecium velutinum group
- Brachythecium velutinum-Polytrichadelphus lyallii association

Brachythecium collinum group
- Brachythecium collinum-Dicranoweisia crispula association

Tortula ruralis group

Bryophyte associations are summarized in Table 1.

Aulacomnium palustre Group

The wettest sites in the study area supported the *Aulacomnium palustre* group. These sites occur on seeps or near springs where water tables are close to the surface most of the year. These sites are also relatively cool and humid for the area and always support *Abies lasiocarpa* and *Picea engelmannii.*

Three bryophyte associations were recognized in the *Aulacomnium palustre* group. All three associations had a relatively high coverage of *Aulacomnium palustre* but differed in bryophyte and vascular species composition, wetness of the site, and habitat type.

Aulacomnium palustre-Bryum weigelii Association (Table 1). The wettest sites in the *Aulacomnium* group are dominated by *Aulacomnium palustre*, *Bryum weigelii*, and *Campylium stellatum.* This association occurs mainly at upper elevations where seeps or springs provide moisture throughout the dry season. It was always found in the *Abies lasiocarpa/Caltha biflora* habitat type (h.t.) that supports a rich assortment of wet site forbs. In these hydric sites, dense mats of *Bryum weigelii* and *Campylium stellatum* dominate in slight depressions but codominate with *Aulacomnium palustre* on the level microrelief. With slightly less moisture, *Campylium stellatum* decreased in coverage while *Aulacomnium palustre* increased. Coverage values averaged 5 percent for *Aulacomnium palustre*, 10 percent for *Bryum weigelii* and 2 percent for *Campylium stellatum.* These three species had 100 percent constancy and both the *Bryum weigelii* and *Campylium stellatum* were found exclusively in this association. Other bryophytes common to this association and indicating its hydric environment are *Drepanocladus aduncus*, *D. uncinatus*, *Philonotis capillaris*, *P. fontana* var. *pumila*, and *Rhizomnium perssonii.*

Aulacomnium palustre-Amblystegium juratzkanum Association (Table 1). This association was found only on broad gentle stream terraces that have a high water table throughout the year. It appeared restricted to the *Picea engelmannii/Carex disperma* h.t. which supports a layer of grasses and sedges. The combination of *Aulacomnium palustre*, *Amblystegium juratzkanum*, and *Tetraphis pellucida* indicates this association. Average coverages were 3.5 percent for *Aulacomnium palustre* and 0.4 percent for *Am-*

TABLE 1. Average coverage and constancy values for species in the major moss groups and associations.
(Numbers to left of parentheses indicate average coverage; within parentheses, percent constancy; . = not present.)

Major moss group or association	Group total	Aulacomnium palustre group: Aulacomnium palustre-Bryum weigelii association	Aulacomnium palustre group: Aulacomnium palustre-Amblystegium juratzkanum association	Aulacomnium palustre-Brachythecium velutinum association	Brachythecium velutinum group total	Brachythecium velutinum group: Brachythecium velutinum-Polytrichadelphus lyallii association	Brachythecium collinum group total	Brachythecium collinum group: Brachythecium collinum-Dicranoweisia crispula association	Tortula ruralis group total
Number of plots (n)	n=13	n=3	n=3	n=7	n=11	n=6	n=51	n=29	n=5
MOSSES									
Amblystegium juratzkanum	0.0(31)	0.0(33)	0.4(100)	.	.	.	.	.	.
Aulacomnium palustre	7.0(100)	5.0(100)	3.5(100)	9.0(100)	.	.	.	.	.
Brachythecium collinum	0.0(38)	0.0(33)	0.0(67)	0.0(28)	0.003(82)	0.007(67)	2.0(96)	2.0(93)	.
Brachythecium erythrorrhizon	0.7(31)	2.0(67)	0.0(33)	0.6(14)	.	.	.	.	.
Brachythecium hylotapetum	0.07(8)	.	.	0.1(14)	0.0006(18)	.	0.1(2)	0.2(3)	.
Brachythecium salebrosum	0.0(15)	.	0.0(33)	0.0(14)	.	.	0.02(4)	0.03(7)	.
Brachythecium starkei	0.0(8)	0.0(33)	.	.	.	.	.	.	.
Brachythecium velutinum	4.0(69)	.	0.4(67)	7.0(100)	3.0(100)	5.0(100)	.	.	.
Bryum caespiticium	.	.	.	.	0.0(9)	.	0.0(6)	0.0(10)	0.0(20)
Bryum creberrium	.	.	.	.	.	.	0.0(2)	.	0.0(20)
Bryum pallescens	0.0(8)	0.0(33)	.	.	.	.	0.0(6)	0.0(3)	.
Bryum sandbergii	0.0(8)	.	.	0.0(14)	0.0(18)	0.0(17)	0.0(6)	0.0(3)	.
Bryum weigelii	2.0(23)	10.0(100)	.	.	.	.	.	.	.
Bryum sp.	0.05(38)	0.1(33)	0.0(33)	0.04(43)	0.0003(27)	0.05(33)	0.1(63)	0.2(65)	0.01(60)
Calliergonella cuspidata	0.0(15)	.	0.0(33)	0.0(14)	.	.	.	.	.
Campylium stellatum	0.4(23)	2.0(100)	.	.	.	.	.	.	.
Ceratodon purpureus	0.0(8)	.	0.0(33)	.	0.002(54)	0.007(33)	0.1(43)	0.007(34)	0.0(20)
Desmatodon latifolius	.	.	.	.	.	.	0.0(2)	0.0(3)	.
Dicranoweisia crispula var. contermina	0.0(8)	.	0.0(33)	.	0.0(9)	.	0.1(55)	0.2(93)	.
Dicranum tauricum	0.0(23)	.	0.0(100)	.	0.0(9)	.	0.006(6)	0.01(7)	.
Drepanocladus aduncus	0.3(15)	1.0(67)	.	.	.	.	.	.	.
Drepanocladus uncinatus	0.5(54)	2.0(67)	0.0(100)	0.1(28)	.	.	0.06(2)	.	.
Encalypta vulgaris	.	.	.	.	.	.	0.06(14)	0.0(21)	0.0(60)
Grimmia alpestris	.	.	.	.	0.0(9)	0.0(17)	0.0(8)	0.0(3)	.
Grimmia alpicola	.	.	.	.	.	.	0.0(2)	.	.
Grimmia apocarpa	.	.	.	.	.	.	.	.	.
Grimmia calyptrata	.	.	.	.	.	.	0.0(10)	0.0(17)	.
Grimmia sp.	.	.	.	.	.	.	0.001(10)	0.002(10)	.

TABLE 1. (Continued)

Major moss group or association	Group total	Aulacomnium palustre-Bryum weigelii association	Aulacomnium palustre-Amblystegium juratzkanum association	Aulacomnium palustre-Brachythecium velutinum association	Group total	Brachythecium velutinum-Polytrichadelphus lyallii association	Group total	Brachythecium collinum-Dicranoweisia crispula association	Group total
Helodium blandowii	0.0(8)	.	.	0.0(14)	.	.	.	.	.
Hypnum revolutum	0.02(15)	0.0(33)	.	0.04(14)	.	.	0.02(16)	0.03(27)	0.0(20)
Leptobryum pyriforme	0.0(8)	.	.	0.0(14)	.	.	.	.	.
Mnium blyttii	0.9(8)	.	4.0(33)	.	.	.	.	.	.
Orthotrichum consimile	.	.	.	.	.	.	0.0(6)	0.0(10)	0.0(20)
Orthotrichum laevigatum	.	.	.	.	.	.	0.0(4)	0.0(7)	0.0(20)
Orthotrichum speciosum	0.0(8)	.	0.0(33)	.	.	.	0.0(2)	.	.
Orthotrichum sp.	.	.	.	.	.	.	0.0(4)	0.0(7)	.
Philonotis capillaris	0.02(8)	0.1(33)	.	.	.	.	.	.	.
Philonotis fontana pumila	0.0(8)	0.0(33)	.	.	.	.	.	.	.
Plagiomnium insigne	2.0(31)		3.0(67)	3.0(28)	.	.	.	.	.
		Aulacomnium palustre group			Brachythecium velutinum group		Brachythecium collinum group		Tortula ruralis group
Number of plots (n)	n=13	n=3	n=3	n=7	n=11	n=6	n=51	n=29	n=5
MOSSES									
Pleurozium schreberi	0.0(8)	.	0.0(33)	.	.	.	.	.	.
Pohlia cruda	0.0(15)	0.0(33)	0.0(33)	.	.	.	.	.	0.0(20)
Pohlia drummondii	0.0(8)	0.0(33)	.	.	.	.	.	.	.
Pohlia nutans	1.0(91)	0.6(67)	3.0(100)	0.9(100)	0.0003(64)	0.05(67)	0.3(37)	0.3(38)	.
Polytrichadelphus lyallii	0.005(15)	0.0(33)	.	0.007(14)	2.0(54)	3.0(100)	0.3(25)	0.2(17)	.
Polytrichum juniperinum	0.04(23)	.	.	0.08(43)	0.0(27)	.	0.2(29)	0.01(24)	10.0(20)
Polytrichum piliferum	0.0(15)	.	0.0(33)	0.0(14)	0.0003(18)	0.05(33)	0.001(10)	0.002(7)	.
Rhizomnium perssonii	0.008(23)	0.03(67)	0.0(33)	.	.	.	.	.	.
Sphagnum fimbriatum	0.0(15)	0.0(33)	0.0(33)	.	.	.	.	.	.
Tetraphis pellucida	0.0(23)	.	0.0(100)	.	.	.	.	.	.
Timmia austriaca	0.6(8)	.	3.0(33)	.	.	.	0.0(2)	0.0(3)	.
Timmia megapolitana	.	.	.	.	.	.	0.006(4)	0.0(3)	.
Tortula norvegia	.	.	.	.	.	.	0.0(4)	0.0(7)	.
Tortula ruralis	0.0(8)	.	.	.	0.0(36)	.	2.0(67)	3.0(86)	6.0(100)

blystegium juratzkanum. Tetraphis pellucida acts as an indicator by its mere presence. It was found only in this association on moist, well-decayed wood. All three indicator species have 100 percent constancy in this association. Other bryophytes having high constancies are the mosses *Plagiomnium insigne*, *Dicranum tauricum*, *Drepanocladus uncinatus*, and *Pohlia nutans*, and the hepatic *Lophozia ventricosa.*

Aulacomnium palustre-Brachythecium velutinum Association (Table 1). This association denotes the driest sites found in the *Aulacomnium palustre* group. It occurs on cool moist stream terraces which support the *Abies lasiocarpa/Calamagrostis canadensis* h.t. and the *Abies lasiocarpa/Vaccinium caespitosum* h.t., *Calamagrostis canadensis* phase. The *Calamagrostis* is usually well represented in both vascular associations, but presence of the *Vaccinium* was not accompanied by any noticeable change in bryophyte composition.

In this association *Aulacomnium palustre* reaches a coverage of 9 percent, with *Brachythecium velutinum* averaging 7 percent. Though it may dominate elsewhere, *B. velutinum* only codominates with *A. palustre* in this association. On wetter sites, *B. velutinum* has a low coverage, possibly because it cannot compete with the wet site mosses.

The only other bryophyte with high constancy in this association, *Pohlia nutans*, was not a useful indicator for any of the associations because of its wide range in elevation and habitat.

Brachythecium velutinum Group

Brachythecium velutinum extends into drier habitats than *Aulacomnium palustre* occupies. So, as *A. palustre* reaches its dry limits, *B. velutinum* becomes the dominant bryophyte and forms the basis for this group. The *Brachythecium velutinum* group is found on cool, well-drained uplands dominated by *Abies lasiocarpa* or *Pseudotsuga menziesii.* The understory dominants are *Vaccinium scoparium* and *Calamagrostis rubescens*, or both. Hepatics are limited to isolated occurrences. Bryophyte associations are not as distinct in this group as in the *Aulacomnium palustre* group and only one association could be recognized.

Brachythecium velutinum-Polytrichadelphus lyallii Association (Table 1). This association is dominated by *Brachythecium velutinum* and *Polytrichadelphus lyallii*, which have average coverages of 5 and 3 percent, respectively. It occurs on moderately steep slopes in the study area and is restricted to the *Abies lasiocarpa/Vaccinium scoparium* h.t. Both indicator species were found growing only on soil, with *Polytrichadelphus lyallii* often forming dense mats 15-30 cm wide in open areas, but giving way to isolated plants under *Vaccinium scoparium. Brachythecium velutinum* coverage was highest under moderately dense canopies of *Vaccinium scoparium* but was greatly reduced under dense canopies.

A number of stands in the *Brachythecium velutinum* group did not have *Polytrichadelphus lyallii* and had low coverages of *B. velutinum.* Therefore they were not included in the *Brachythecium velutinum-Polytrichadelphus lyallii* association. Also, these stands did not occur in the *Abies lasiocarpa/Vaccinium scoparium* h.t. except one that had high coverages of *Calamagrostis rubescens.* Instead, these stands occurred in either the *Abies lasiocarpa/Calamagrostis rubescens* or *Pseudotsuga menziesii/Calamagrostis rubescens* h.t.

Brachythecium collinum Group

The drier habitats of the study area apparently lack enough surface moisture to support many of the mosses and hepatics found on other sites. Here, the drought-tolerant *Brachythecium collinum* becomes the dominant bryophyte and denotes the *B. collinum* group. This group encompasses the largest part of the study area and contains several drought-tolerant vascular associations. I defined only one bryophyte association in this group.

Brachythecium collinum-Dicranoweisia crispula Association (Table 1). The *Brachythecium collinum-Dicranoweisia crispula* var. *contermina* association is dominated by *B. collinum* and *D. crispula* var. *contermina*, which have 2 and 0.2 percent average coverage, respectively. *B. collinum* was found growing on soil, on soil over rocks, and at the interface between rock and soil. *Dicranoweisia crispula* var. *contermina* was found growing on soil over rock and on rotting wood. *Tortula ruralis* was often found in this association and had an average coverage of 3 percent. However, it did not appear indicative of this association because it extends into much drier habitats than either of the two indicator species.

The most common habitat types supporting this association were *Pseudotsuga menziesii/Arnica cordifolia*, *Abies lasiocarpa/Arnica cordifolia*, *Pseudotsuga menziesii/Juniperus communis*, and *Abies lasiocarpa/Juniperus communis*. All of these sites are characterized by severe dry conditions much of the year. Other habitat types in which this association was found include *Abies lasiocarpa/Calamagrostis rubescens*, *Pseudotsuga menziesii/Calamagrostis rubescens*, *Pseudotsuga menziesii/Festuca idahoensis*, *Pseudotsuga menziesii/Symphoricarpos oreophilus*, and *Pseudotsuga menziesii/Spiraea betulifolia* h.t., *Calamagrostis rubescens* phase.

Stands in the *Brachythecium collinum* group which are not part of the *Brachythecium collinum-Dicranoweisia crispula* var. *contermina* association lack *Dicranoweisia* and are dominated only by *B. collinum*. Vascular vegetation found on these sites indicated several habitat types: *Abies lasiocarpa/Carex geyeri*, *Abies lasiocarpa/Arnica cordifolia*, *Pseudotsuga menziesii/Calamagrostis rubescens*, and *Pseudotsuga menziesii/Juniperus communis*.

Tortula ruralis had a lower coverage and constancy in stands dominated only by *Brachythecium collinum* than it had in the *Brachythecium collinum-Dicranoweisia crispula* var. *contermina* association.

Tortula ruralis Group

Tortula ruralis dominates xeric stands in the study area, with an average coverage of 6 percent. Other species that are often present but have lower coverages are *Encalypta vulgaris* and *Bryum* species. The low number of bryophytes in this group reflects the general paucity of the bryophyte flora on xeric soils in this area.

The *Tortula ruralis* group (Table 1) was found only in the *Pseudotusga menziesii/Festuca idahoensis* h.t. However, because high coverages of *Tortula ruralis* extend into many dry nonforested sites of central Idaho, this species probably is a major component of habitat types not included in this study.

Other Bryophyte-Vascular Plant Relationships

On glaciated valley floors and glacial outwash plains, pure stands of *Pinus contorta* dominate a thin understory of *Festuca idahoensis*. These dry cold sites also support a depau-

perate moss layer consisting of various species. However, the species present were always members of the Polytrichaceae. Either *Polytrichum piliferum*, *P. juniperinum*, or *Polytrichadelphus lyallii* were present on these sites. Sites with *P. lyallii* appeared restricted to elevations above 2000 m (6562 ft).

Other habitats encountered in the study area but not included in the major moss groups occurred at elevations over 2700 m (8859 ft). Here *Pinus albicaulis* and deformed *Abies lasiocarpa* codominated a variety of understories, most of which were dominated by either *Festuca idahoensis*, *Juncus parryi*, or *Lupinus argenteus*. Members of the Polytrichaceae again dominated a community of sparse bryophytes; *Polytrichadelphus lyallii* occurs in many stands and has an average coverage of 3 percent.

These habitats have similar conditions that appear to be related to the establishment of Polytrichaceae and the absence of other bryophytes. They are: (1) low average temperature with nightly frost throughout much of the growing season, and (2) mineral soil having little protection by litter or a vascular plant canopy. These two conditions are conducive to extensive frost action, which continually disturbs the soils and possibly has an adverse effect on many bryophytes. *Polytrichum piliferum*, however, can tolerate frost heaving and can even form moss mats under yearly disturbance (Marsh, 1972).

Epiphytic Bryophytes

True epiphytic bryophytes were those growing on trees or shrubs but not in a position to utilize soil moisture or nutrients. *Dicranum tauricum* was the only true epiphytic bryophyte found in the study plots. Bryophytes growing on tree roots and bases within approximately 5 cm of the ground were not considered true epiphytes because their independence of soil moisture and nutrients could not be verified. These species included *Dicranum tauricum*, *Dicranoweisia crispula* var. *contermina*, *Pohlia nutans*, *Orthotrichum consimile*, and *O. speciosum*.

Discussion

Bryophytes and Moisture Tolerance

Within the study area, moisture appears to be the limiting factor for most bryophytes. At the hydric end of the scale and into the wet mesic sites, the *Aulacomnium palustre* group dominates. The *Brachythecium velutinum* group best represents the mesic segment. Dry or mesic sites are represented by the *Brachythecium collinum* group. Only the *Tortula ruralis* group extends into the xeric segment of the moisture gradient. In the hydric to moist mesic segments, moss associations are restricted to specific habitat types (Table 2). For example, the *Aulacomnium palustre-Bryum weigelii* association occurs only in the *Abies lasiocarpa/Caltha biflora* habitat type and the *Aulacomnium palustre-Amblystegium juratzkanum* association occurs only with *Picea engelmannii/Carex disperma*. But as sites become drier, moss associations span several habitat types. For example, the *Brachythecium collinum-Dicranoweisia crispula* var. *contermina* association occurs in nine different habitat types (Table 2).

Xeric species were often found in mesic habitats but were on dry microsites such as rocks, tree bases, and hummocks. However, the moist site dominants were seldom found in dry habitats. As a result, species richness was highest in the wet sites.

Differences in the moisture regime also appear to affect the type of substrate on which some mosses grow. The widespread *Pohlia nutans* grows mostly on soil and forest

TABLE 2. Moss associations and their relationship to vascular associations.

Aulacomnium palustre group
Aulacomnium palustre-Bryum weigelii association with Abies lasiocarpa/Caltha biflora association
Aulacomnium palustre-Amblystegium juratzkanum association with Picea engelmannii/Carex disperma
Aulacomnium palustre-Brachythecium velutinum association with Abies lasiocarpa/Calamagrostis canadensis association Abies lasiocarpa/Vaccinium caespitosum association Calamagrostis canadensis phase
Brachythecium velutinum group
Brachythecium velutinum-Polytrichadelphus lyallii association with Abies lasiocarpa/Vaccinium caespitosum association
Brachythecium collinum group
Brachythecium collinum-Dicranoweisia crispula var. contermina association with Abies lasiocarpa/Calamagrostis rubescens association Abies lasiocarpa/Arnica cordifolia association Abies lasiocarpa/Juniperus communis association Pseudotsuga menziesii/Calamagrostis rubescens association Pseudotsuga menziesii/Arnica cordifolia association Pseudotsuga menziesii/Juniperus communis association Pseudotsuga menziesii/Spiraea betulifolia association Calamagrostis rubescens phase Pseudotsuga menziesii/Symphoricarpos oreophilus association Pseudotsuga menziesii/Festuca idahoensis
Tortula ruralis group
Tortula ruralis (no defined association) with Abies lasiocarpa/Carex geyeri Pseudotsuga menziesii/Festuca idahoensis

duff in wet habitats of the *Aulacomnium palustre* and *Brachythecium velutinum* groups, yet it grows mostly on decaying wood in drier habitats supporting the *Brachythecium collinum* group. Among the many factors that may account for this change in substrate between habitats, moisture availability appears the most likely one.

Bryophytes as Indicators

In the study area, bryophytes appear to have little value as indicators of subunits within vascular plant associations. This finding is probably due to the low diversity of dry site mosses in the area and their wide ecological amplitude. Because the study area contains few hydric and mesic habitats, lichens, which are generally more drought tolerant than mosses (Barkman, 1958), may better delineate smaller ecological units within the drier habitat types. However, on hydric and mesic sites, bryophytes can be used as indicators of moisture conditions (Stringer and Stringer, 1974) and pH (Jeglum, 1971).

Bryophyte Taxonomy

Moss specimens in the study area were identified to variety whenever possible, but lack

of sexual reproductive organs and sporophytes prevented variety distinction for nearly all specimens. Collections of *Brachythecium velutinum* with sporophytes were identified as *B. velutinum* var. *velutinum*, but the many vegetative collections could not be identified to variety. Differences in moss associations and vascular associations could not be distinguished between plots with variety distinctions and plots with only species distinction. To facilitate synthesis, the variety distinctions were dropped and all specimens were left at the species level of identification.

Dicranoweisia crispula specimens, however, consistently had sporophytes and could be identified to the variety *contermina*. This varietal distinction was retained in the association synthesis and descriptions.

Where sporophyte characteristics determine variety, varietal distinction remains a problem for bryologists constructing association relationships. To circumvent this problem I retained variety distinctions when they occurred consistently but dropped them when they failed to show any association differences.

Bryophyte Succession

We know relatively little about growth rates and successional patterns of bryophytes as compared to those of vascular plants. However, because most climax forests have undergone a period of dense canopy cover, the bryophyte association should represent the most shade-tolerant species adapted to the site. Opportunistic bryophytes, species quick to invade unoccupied sites, would occur primarily on disturbed microsites such as fallen tree limbs, newly exposed rock and soil from uprooted trees, animal burrows, and so on. These species can easily invade newly disturbed sites because of their wide dispersal, broad ecologic tolerance, and high reproductive rates (Slack, 1971).

Moss species occurring throughout the study area which I consider opportunistic in many habitats include *Ceratodon purpureus*, *Bryum caespiticium*, *Polytrichum juniperinum*, and *P. piliferum*. These species often dominated disturbed situations and had low coverages on sites with little disturbance. On drier sites, however, these species may achieve climax status through lack of replacement by less drought-tolerant mosses. It is possible, then, that opportunistic bryophytes found in moist habitats may form climax associations on drier sites.

Conclusion

Four moss groups characterize the bryophyte flora of forest ecosystems in east-central Idaho. Within these four groups, five bryophyte associations correlate with the habitat type classification (Steele *et al.*, 1975, Habitat types of central Idaho, review draft, Intermountain Station). These five associations were named for those bryophytes having the highest coverages and greatest indicator value.

The *Aulacomnium palustre* group with its three associations indicates three different hydric habitats. The *Aulacominum palustre-Bryum weigelii* association found around seeps and springs occurs exclusively in the *Abies lasiocarpa/Caltha biflora* h.t. *Aulacomnium palustre-Amblystegium juratzkanum* is restricted to stream bottoms supporting a *Picea engelmannii/Carex disperma* h.t. The *Aulacomnium palustre-Brachythecium velutinum* association occurs in habitats with high water tables which support either the *Abies lasiocarpa/Calamagrostis canadensis* h.t. or the *Abies lasiocarpa/Vaccinium caespitosum* h.t., *Calamagrostis canadensis* phase.

The *Brachythecium velutinum* group and its only defined association, *Brachythecium velutinum-Polytrichadelphus lyallii* indicate mesic habitats. This association was found in cool, well-drained uplands supporting the *Abies lasiocarpa/Vaccinium scoparium* h.t.

The *Brachythecium collinum* group, the *Brachythecium collinum-Dicranoweisia crispula* var. *contermina* association, and the *Tortula ruralis* group indicate the drier environments. The *Brachythecium* group and its accompanying association occur throughout a number of different habitat types. The *Tortula ruralis* group is associated with only the *Pseudotsuga menziesii/Festuca idahoensis* h.t., but it also occurs in dry nonforested habitats.

All moss groups except the *Aulacomnium palustre* group contained some stands that did not fit into a definite bryophyte association and thus remain undefined within the group. These stands were placed in the groups they best represented, depending on the bryophytes that appeared to be dominant. Future studies of bryophyte communities in forests surrounding the study area may reveal other associations that will help clarify the status of these unclassified stands.

Relationships between the vascular plants and moss associations suggest that mosses may be used to indicate levels of moisture availability. Many moisture-sensitive mosses occur on various wet sites; it appears they may have some indicative value at the hydric end of the moisture gradient. However, our present data are still inadequate for practical applications.

Literature Cited

Barkman, J. J. 1958. Phytosociology and Ecology of Cryptogamic Epiphytes. Van Gorcum Co., Assen, Netherlands. 628 pp.

Becking, R. W. 1954. Site Indicators and Forest Type Classification of Douglas Fir Region in Western Washington and Oregon. Univ. of Wash., Seattle. Ph.D. Thesis. 134 pp.

Cooke, W. B. 1955. Fungi, lichens and mosses in relation to vascular plant communities in eastern Washington. Ecol. Monogr. 25:119-180.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northw. Sci. 33:50-57.

————, and J. B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Wash. Agric. Exp. Stn. Tech. Bull. 60. Wash. State Univ., Pullman. 104 pp.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, Pac. Northwest For. and Range Exp. Stn., Portland, Oreg. 417 pp.

Hoffman, G. R., and R. G. Kazmierski. 1969. An ecological study of bryophytes and lichens on *Pseudotsuga menziesii* on the Olympic Peninsula, Washington. 1. A description of the vegetation. The Bryol. 72:1-19.

Jeglum, J. K. 1971. Plant indicators of pH and water levels in peatlands at Candle Lake, Saskatchewan. Can. J. Bot. 49:1661-1676.

Krajina, V. J. 1965. Biogeoclimatic zones and classification of British Columbia. Ecology of North America, Vol. 1: 11-17. University of British Columbia, Vancouver, B.C.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Hattori Botanical Laboratory, Miyazaki- Ken, Japan. 362 pp.

Looman, J. 1964. Ecology of lichen and bryophyte communities in Saskatchewan. Ecology 45:481-491.

McCleary, J. A., and V. V. Green. 1971. A checklist of Idaho mosses. The Bryol. 74:175-180.

Marsh, W. M. 1972. Role of moss in slope formation. Ecology 53:489-493.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York. 547 pp.

Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34. Intermt. For. and Range Exp. Stn., Ogden, Utah. 174 pp.

Slack, N. G. 1971. Species Diversity and Community Structure in Bryophytes. State Univ. New York, Ph.D. Thesis.

Soil Conservation Service. 1965. Mean annual precipitation—State of Idaho. Isohyet map M-4358. U.S. Dep. Agric., Portland, Oreg.
Spilsbury, R. H., and D. S. Smith. 1947. Forest Site Types of the Pacific Northwest. B. C. Dep. Lands and For. Tech. Publ. T-30. 46 pp.
Steele, A. M. 1974. Moss Communities of Central Idaho Forests. Univ. of Idaho, Moscow, Master of Sci. thesis. 52 pp.
Stringer, P. W., and M. H. L. Stringer. 1974. Studies on the bryophytes of southern Manitoba. VI. An ecological study of the bryophytes of coniferous forests in Bird's Hill Provincial Park. The Bryol. 77:1-16.

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Reproduction, Growth, and Development of the Mountain Beaver (Aplodontia rufa pacifica)[2]

Abstract

This paper presents a summary of observations of the growth, development, and behavior of two mountain beavers born in captivity and raised for 68 days. Initial growth was rapid, and the mean weight of the young increased from 19.8 g at two days to 364 g at 60 days, or 43 percent of adult mean weight. The most rapid growth was during weeks seven and eight, coincident with weaning. Death was attributed to a bacterial infection.

Introduction

A search of the literature revealed few references to the young of *Aplodontia.* Cramblet and Ridenhour (1956) observed the birth of three young to a captive female and reported briefly on the first five days of their development. Our information is based on examination of Pacific mountain beaver (*Aplodontia rufa pacifica*) periodically live-trapped in the field and on daily observation of a litter raised in captivity.

Two female mountain beavers gave birth to litters of four and two young in captivity. Both pregnant females were live-trapped about one week before parturition, in the Coast Range of western Oregon. The litter of four, born on 31 March 1966, survived for five weeks. They were not handled for fear of rejection by the female. The litter of two, born on 3 April 1966, were observed and weighed daily on a Mettler balance. The female tolerated the handling of the young.

Breeding Habits, Males

The testes of mountain beaver are abdominal, except during the breeding season when they become semiscrotal. Pfeiffer (1956) found the testes reached maximum size in January and February. Hubbard (1922), in Washington, noted that the testes began to enlarge about 15 December, attained full size by 15 January, began to decline early in April, and regained nonbreeding size by mid-April. We first observed wild males with

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semiscrotal testes in late December, when both males and females began discharging a cloudy yellowish-milky urine while confined in a handling cage. By mid-January, most mature males had descended testes that remained semiscrotal until near the end of March, when they again became abdominal.

Breeding Habits, Females

The breeding season of *Aplodontia* is short and fairly well defined. Pfeiffer (1958) determined that estrus occurs within a period of five to seven weeks in winter, and all of the breeding females in a population ovulate about the same time each year. Female mountain beavers do not bear young before their second season.

Females in estrus have hypertrophied nipples and a swollen vulva (Pfeiffer, 1958). A circle of black mammary hairs around the nipples also becomes prominent in pregnant and lactating females (Pfeiffer, 1955). The earliest sign of estrus we observed was in early February when the urinary papillae of two captured mature females appeared red and swollen.

Hubbard (1922) reported taking a pregnant female in late February near Seattle, Washington. Early stages of pregnancy were observed by Scheffer (1929) in late March, and 11 of 26 females that he examined in early April were pregnant. Mountain beaver examined by Pfeiffer (1958) in western Washington had early embryos during late February and gave birth by mid-March. Parturition was reported by Cramblet and Ridenhour (1956) to occur about the same time in northwestern California as the birth of the two litters reported here.

Litter Size

Scheffer (1929) examined 16 pregnant females and reported seven with litters of two young and nine with litters of three. Dalquest (1948) reported the litter size of mountain beavers in Washington to be from two to three and, rarely, four. Pfeiffer (1958) examined 12 pregnant females and found an average of 2.4 embryos.

Lactation

Pfeiffer (1958) believed that lactation in *Aplodontia* probably does not continue beyond two months. Hubbard (1922) reported taking lactating females in May. Voth (1968) reported females lactating from late April to late June. Our field records show females lactating from early April through late May. One of our captive females was still lactating at the end of May.

Physical Development and Behavior

Newborn *Aplodontia* were helpless and appeared embryonic or premature (Fig. 1). The skin was pink, slightly wrinkled, and naked except for the presence of vibrissae. Eyes and auricular openings were tightly sealed, with the eyes recognizable only as dark spots beneath the skin. The front toes were well developed and equipped with long claws. The hind toes were less developed, and the tail (which remains vestigial) was a mere stub. Sex could be determined by examination of the genitalia.

Only the litter of two was handled. At two days, the weights were 18.0 g and 21.6 g (mean 19.8) with an average body length of 66 mm. These animals were smaller than a litter of three reported by Cramblet and Ridenhour (1956), which averaged 27 g and 87 mm when only one day old. The weight difference between the two remained insigni-

ficant (mean 3.70 g, range 1.8 g to 8.6 g), until day 45 when the eyes of the heavier one opened. The weight difference then increased sharply (mean 21.2 g, range 7.0 to 38.0 g), until day 60, which was four days after the second one had both eyes open. The increased difference in weight was attributed to the increased foraging ability of the one with its eyes open.

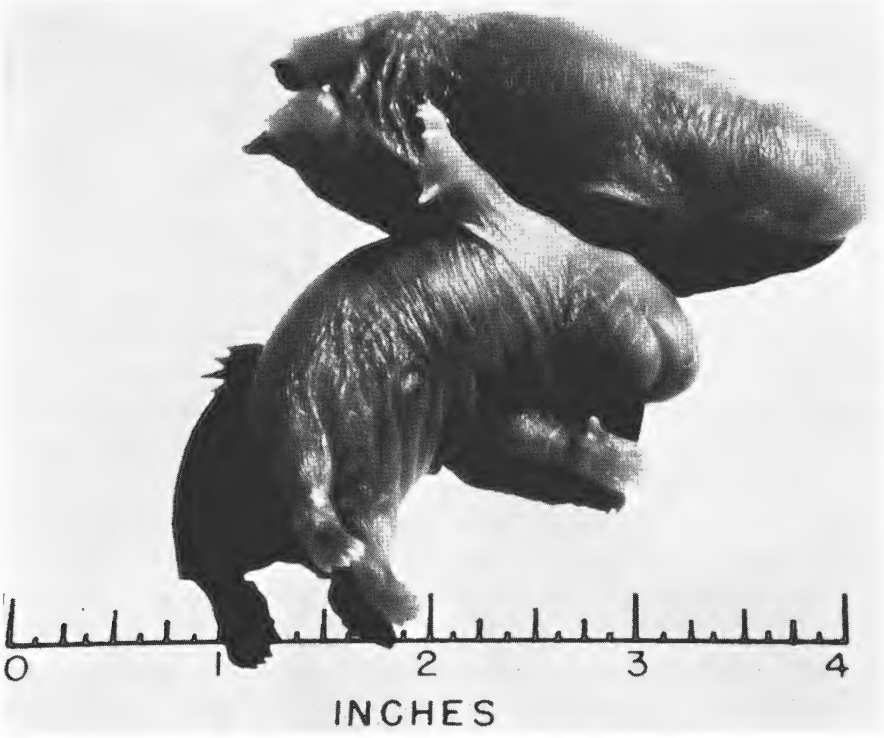

Figure 1. A litter of two *Aplodontia rufa pacifica*, two days old, that were born in captivity on April 3.

At three days, the mountain beavers made squeaking sounds. By day five, dark pigmentation appeared along their backs and the tops of their heads. At seven days, the mean body weight was 27.9 g. Black pigmentation appeared over most of the dorsal surface, and the skin became increasingly wrinkled and baggy over the hindquarters. A sparse growth of fine hairs covered most of the body at nine days. The ear pinnae unfolded and became erect, and the eye slits formed at day ten, but both eyes and ears remained closed.

At 14 days, the body was completely covered with hair. The hair on the dorsal surface was dark and sleek, and that on the ventral side was white. At 15 days, the mountain beavers began to crawl with only the more developed front legs (Fig. 2). At 21 days, the mean body weight was 73.8 g, and the length was 125 mm. The ears were now opened. Hair on the dorsal surface became darker and more glossy; a brownish color appeared on the neck and shoulders and along both flanks.

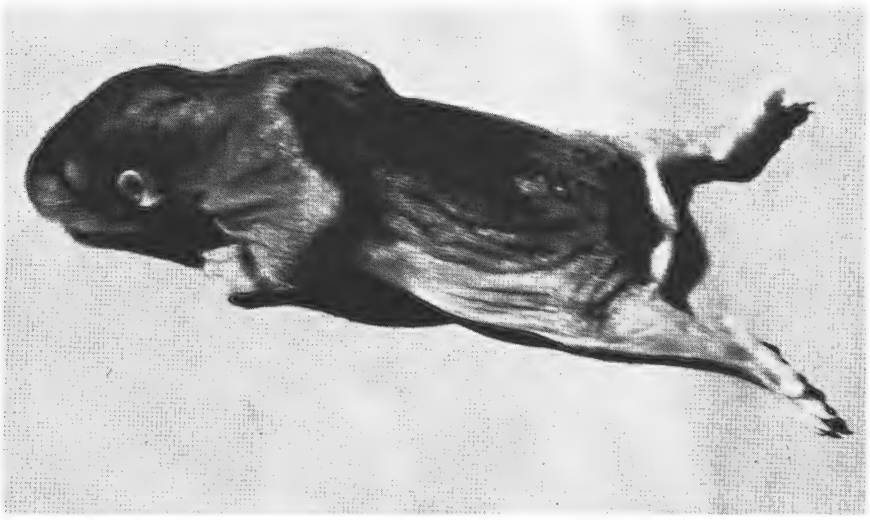

Figure 2. One of a litter of two young *Aplodontia rufa pacifica* at 15 days of age. Only the more developed front legs are used in crawling at this age. Note thick dark hair on dorsal surface.

At four weeks, the lower incisors erupted and, five days later, the upper incisors erupted. At this time, one of the young was observed scratching its lower jaw with the right hind foot.

Coordination of the young mountain beavers improved considerably during week five. They were able to hold up their heads and also use their hind legs for crawling. Balance was poor, and they still had difficulty in righting themselves. Investigative behavior was exhibited through sniffing, licking, and nibbling themselves and the fingers of the handler, and they made their first attempts at face grooming. The first solid food, rolled oats, was eaten on day 38.

On day 45, when the larger animal weighed 190 g, the eyes opened. The smaller animal weighed 184 g, and the eyes remained closed. The mean total length of the beavers was 210 mm. The eyes of the second animal did not open until day 54, when the animal weighed 280 g. In comparison, the young of *Spermophilus lateralis* open their eyes at 27-31 days (McKeever, 1964), and *Spermophilus beecheyi* opens its eyes at days 34-37 (Tomich, 1962). Our mountain beavers roamed freely about their cage. When both were placed on a table, the one with its eyes opened avoided falling off the edge, but the one with eyes closed did not. They played with each other, biting and pushing with their forepaws.

By week seven, the young readily accepted natural food, such as foliage of red huckleberry (*Vaccinium parvifolium* J. E. Sm.), sword fern (*Polystichum munitum* (Kaulf.) Presl.), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). At eight weeks, both young were still nursing. Their mean body weight was 347 g (337 and 357), a gain of 110 g over the past week. At day 60, they reached a maximum mean weight of 364.5 g (349 and 380). From this point, the young gradually lost weight until their death at 68 days.

Necropsies performed by the Veterinary Diagnostic Clinic at Oregon State University revealed both young *Aplodontia* had intestinal ulcers and a bacterial infection of *Pasteurella* sp. Death was attributed to the infection.

Growth Rate

Mean growth rate of the two young *Aplodontia* raised in captivity from birth to nine weeks is shown in Figure 3. The captive young grew rapidly after their first week. Mean weight was 110 g at four weeks and 347 g at eight weeks. These juveniles experienced their most rapid weight gain during weeks seven and eight. During this two-week period, their weight increased 126 percent over what they had weighed at the end of six weeks. By eight weeks, they had attained about 43 percent of the adult mean weight. Adult mean weight of *A. r. pacifica* is 806 g, based on weights of 75 males and 34 females retrapped and weighed repeatedly during a two-year study in western Oregon (Lovejoy, 1972).

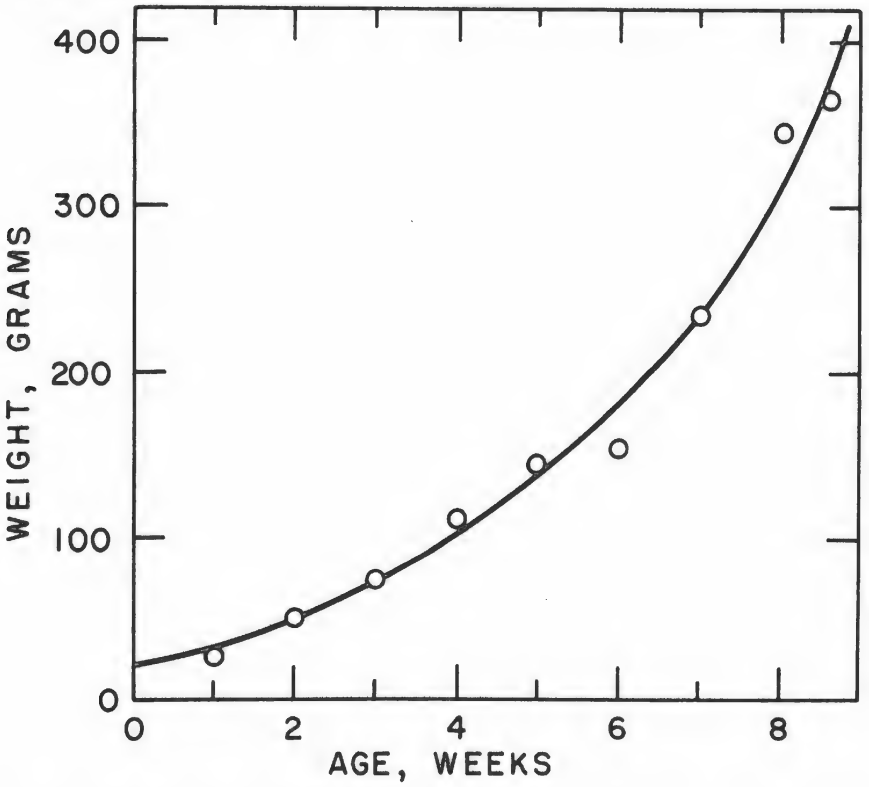

Figure 3. Mean growth rate of two young *Aplodontia rufa pacifica* that were raised in captivity from birth to about 63 days of age.

Literature Cited

Cramblet, H. M., and R. L. Ridenhour. 1956. Parturition in *Aplodontia*. J. Mammal. 37: 87-90.
Dalquest, W. W. 1948. Mammals of Washington. Univ. Kansas Publ., Mus. Natur. Hist. 2: 1-444.
Hubbard, C. A. 1922. Some data upon the rodent *Aplodontia*. Murrelet 3: 14-18.

Lovejoy, B. P. 1972. A Capture-Recapture Analysis of a Mountain Beaver Population in Western Oregon. Oregon State Univ., Corvallis, Ph.D. thesis. 105 pp.
McKeever, S. 1964. Biology of the golden-mantled ground squirrel. Ecol. Monogr. 34: 383-401.
Pfeiffer, E. W. 1955. Hormonally induced "mammary hairs" of a primitive rodent, *Aplodontia rufa.* Anatomical Record 122: 241-256.
————. 1956. The male reproductive tract of a primitive rodent, *Aplodontia rufa.* Anatomical Record 124: 629-635.
————. 1958. The reproductive cycle of the female mountain beaver. J. Mammal. 39: 223-235.
Scheffer, T. H. 1929. Mountain beavers in the Pacific Northwest: their habits, economic status and control. U.S. Dept. of Agric., Farmers' Bull. 1958: 1-18.
Tomich, P. Q. 1962. The annual cycle of the California ground squirrel, *Citellus beecheyi.* Univ. California Publ., Zool. 65: 213-282.
Voth, E. M. 1968. Food Habits of the Pacific Mountain Beaver, *Aplodontia rufa pacifica* Merriam. Oregon State Univ., Corvallis, Ph.D. thesis. 263 pp.

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A Floristic Survey of a Subalpine Meadow on Mt. Wright, Glacier Bay National Monument, Alaska

Abstract

A floristic survey is presented of a subalpine meadow located at an altitude of 640 to 780 m on the northern shoulder of Mt. Wright in Glacier Bay National Monument, Alaska. Topographical and climatic information is included. Three floristically defined vegetation associations are discussed with respect to the plant assemblages and local moisture gradients. At this site the moist, oceanic climate of southeastern Alaska gives rise to subalpine vegetation which is meso-hydric in character. The most common vegetation within the meadow is a lush meltwater association dominated by *Veratrum viride* subsp. *eschscholtzii*, *Lupinus nootkatensis*, and *Heracleum lanatum*.

Introduction

The plant communities of alpine and subalpine zones in western North America have received considerable attention in recent years (Johnson and Billings, 1962; Choate and Habeck, 1967; Bonham and Ward, 1970; Price, 1971; Douglas, 1971; Knapik *et al.*, 1973). Because of the increased use of these areas for public recreation and the fragile nature of such environments with respect to human disturbances (Billings, 1973; Eckholm, 1975), it has become imperative to gain a basic understanding of the structure and functioning of alpine and subalpine communities. This knowledge may provide the insight needed to develop management policies which will ensure the integrity and stability of these communities despite the inevitable increase in use.

Although the arctic tundra of Alaska and northern Canada has also been the subject of investigation (Lindsey, 1953; Drury, 1962), the alpine and subalpine vegetation of the far north has apparently been little studied. Heusser (1954a) reported on the nunatak flora of the Juneau Ice Field, and Cooper (1931, 1939, 1942) presented plant species lists from Glacier Bay National Monument which included alpine collections. Streveler *et al.* (1973) briefly described the alpine meadows of a portion of the outer coast of the Monument and included a species list. However, there has been no floristic survey of a subalpine meadow from this area. These meadows conform to the concept of subalpine vegetation as presented by Löve (1970), and are a common vegetation type on the floors and slopes of glacial cirques and on the shoulders of the coastal mountains of southeastern Alaska. In the Chilkat and Fairweather Ranges which surround Glacier Bay (Fig. 1), subalpine meadows occur at altitudes from 600 to 850 m above

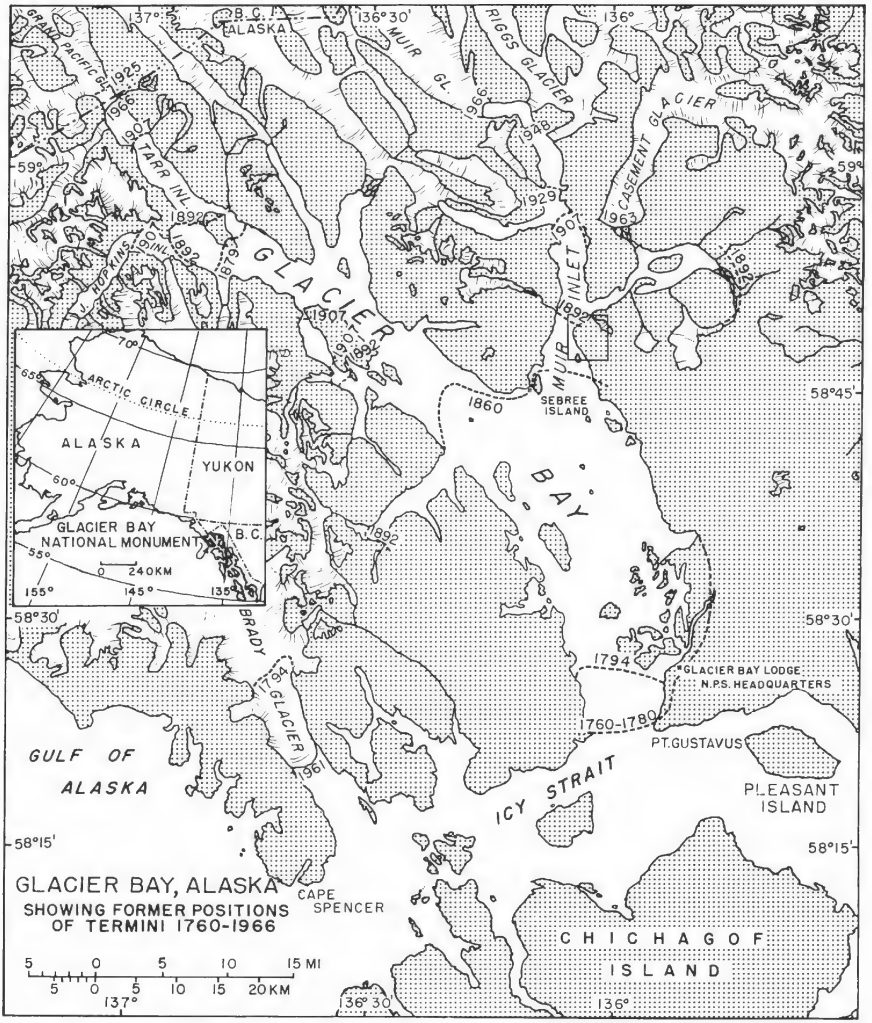

Figure 1. Glacier Bay. The dates indicate the former positions of glacial termini. The Mt. Wright area detailed in Fig. 2 is enclosed by the rectangle in the upper right quarter of the map. American Geographical Society map of 1966, modified from Bohn (1967, p. 109).

sea level. In this paper we describe the vegetation of one such meadow on Mt. Wright in Glacier Bay National Monument.

Environment

The climate of southeastern Alaska is generally described as cool/temperate, rainy, and characterized by long, wet winters and cool summers (Streveler and Paige, 1971). The mean annual temperature is 5 C and the mean annual precipitation is 190 cm for the

National Monument Headquarters at sea level in Bartlett Cove. Winter snows average 4 m in total, but there is seldom more than 2 m accumulation because of frequent rains. Glacier Bay receives a great deal of rain during the entire year; the wettest storms occur in September and October. Bartlett Cove is usually snow-free from early May until October, but the length of the growing season for the Mt. Wright meadow must be much shorter. Using Bartlett Cove temperature data and the adiabatic lapse rate for determining the decrease in temperature with increasing altitude, the average temperature for the period May through mid-October is estimated to be 6.2 C for the meadow: it is 10.3 C at Bartlett Cove. In addition, temperatures tend to be a few degrees cooler in upper Glacier Bay than at Bartlett Cove near the mouth. Loewe (1966) estimates that at an altitude of 900 m the mean annual temperature is 0 C.

Because of the meeting of warm, oceanic air traveling up Glacier Bay and cool air coming off the many glaciers in the northern reaches of the bay, the region is subjected to frequent, dense fogs. The cloudy and foggy conditions cause the actual solar radiation received at the meadow to be substantially less (by about 70 percent) than that potentially available. The high humidity, common foggy conditions, and high precipitation influence the character of the meadow vegetation.

The subalpine meadow lies at an altitude of 640 to 780 m on the northern shoulder of Mt. Wright (Fig. 2). As described in the travelogue of John Muir (1915), Muir Inlet was filled with the ice of the rapidly retreating Muir Glacier in the 1890s. Local perennial snow must have persisted much later. The elevation of the Neoglacial high ice limit (Lawrence, 1977) suggests that the site of the meadow was also glaciated and so represents a relatively new physiographic surface. The presence of *Luzula parviflora*, *Carex pyrenaica*, *Juncus drummondii*, and *Saxifraga punctata* subsp. *pacifica*, which Heusser *et al.* (1954b) consider alpine pioneer species, further indicates a post-Neoglacial development of the meadow vegetation.

The meadow slopes gently (5-10°) to the west and more sharply (30-35°) to the north and east where the mountain shoulder has been subjected to erosion by Dirt Glacier in the valley beyond. At an altitude of 650 m, the west slope drops precipitously to the outwash plain below, the vegetation of which has been described by Noble and Sandgren (1976). A local relief of less than 10 m within the meadow itself consists of rolling ridges and erosional gullies which run predominantly east to west. The till substrate contains a large proportion of fine matrix composed of rock flour, and small, sharp-edged rock fragments. Several bedrock outcroppings protrude through the till mantle.

Methods

Collections were made of the lichen, bryophyte, and vascular flora of the meadow during August of 1974. Three vegetation associations, based upon species composition, relative abundance, uniformity of habitat, and physiognomy, were identified in the field.

Results and Discussion

It was readily apparent that local environmental gradients or "mesotopographic gradients" (Billings, 1973) exist within the meadow. However, the heavy precipitation and frequent foggy conditions tend to override mesotopographic factors such as drainage, aspect, and soil type to some degree and result in less distinction between plant associations than would otherwise be expected.

A very common meltwater association is found in the many hollows and extends

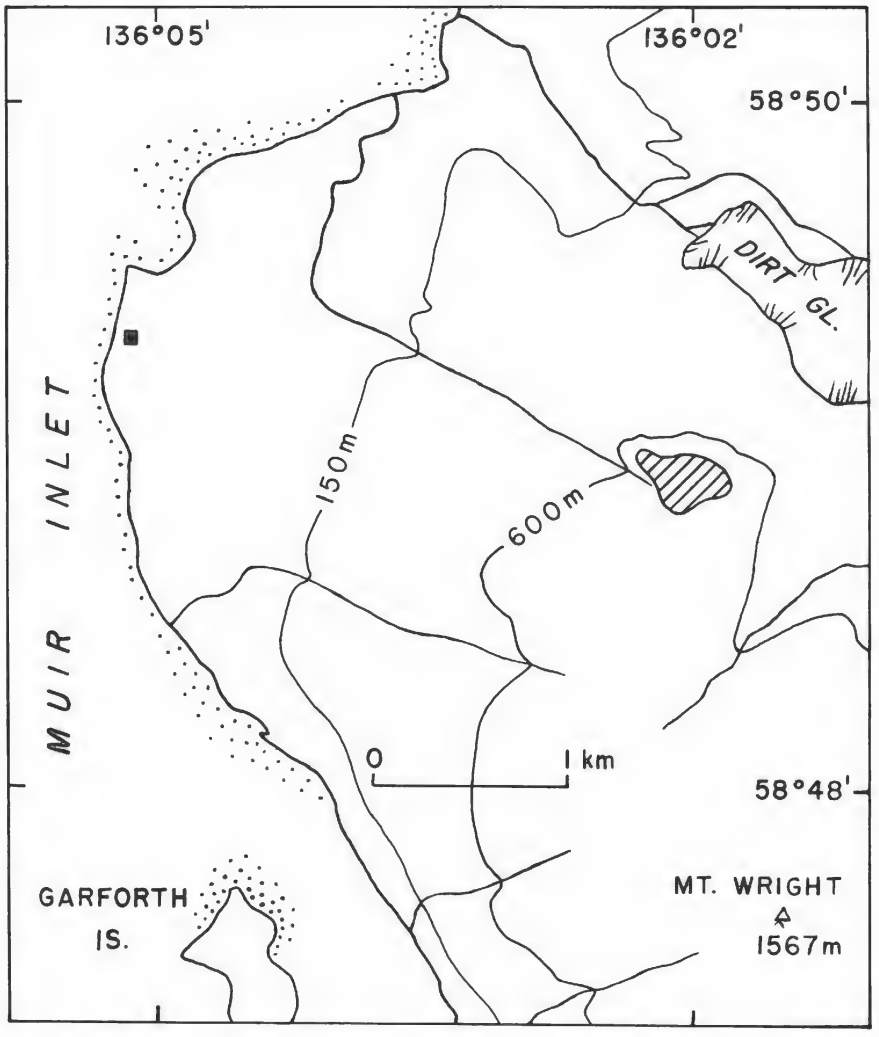

Figure 2. Mt. Wright area. The hatched area indicates the location of the subalpine meadow discussed. The square marks the location of the cabin built by John Muir in 1890.

over the smaller ridges. The dominant plant species include false hellebore (*Veratrum viride* subsp. *eschscholtzii*), Nootka lupine (*Lupinus nootkatensis*), cow parsnip (*Heracleum lanatum*), and a wide variety of smaller alpine flowers. In early August monkshood (*Aconitum delphinifolium* subsp. *delphinifolium*), Langsdorff's violet (*Viola langsdorffii*), buttercups (*Ranunculus eschscholtzii, R. occidentalis* subsp. *occidentalis* var. *brevistylis*), and chickweed (*Stellaria monantha*) were in flower.

This lush meltwater association should be distinguished from the more typical inland alpine tundras commonly referred to as mesic. The colluvial slope meadow habitat occurring on the western slopes of the Cascade Mountains in Washington has a similar species composition (Douglas, 1971) and a similar climatic regime. The three dominant

species that characterize the meltwater association also occur in alpine meadows on the outer coast of Glacier Bay National Monument (Streveler *et al.,* 1973). It would be expected that this meso-hydric subalpine association would be common along the coasts of Washington, British Columbia, and southeastern Alaska with differences in species composition being more strongly influenced by the geographical distribution of plant species than by climate.

The second plant association observed is found on the steep east-facing slope. This slope is well drained and the vegetation low-growing and more sparse than in the meltwater association, as well as being of a different character. Members of the composite family are the dominant plant forms. Common taxa include: *Agoseris glauca,* pussytoe (*Antennaria isolepis*), *Arnica latifolia,* prairie sagewort (*Artemisia frigida*), and goldenrod (*Solidago multiradiata* var. *multiradiata*). Common representatives of other families are bittercress (*Cardamine umbellata*) and *Saxifraga punctata* subsp. *pacifica.*

The well drained, exposed crests of the highest ridges and knolls of the meadow characteristically support shrub and prostrate willows and numerous heaths. Only in this third type of vegetation association are woody species abundant. Such areas were the first sites exposed as the snowcover declined at the end of the Neoglacial. Common taxa include: *Cassiope mertensiana,* mountain heather (*Phyllodoce aleutica* subsp. *glanduliflora*), dwarf blueberry (*Vaccinium caespitosum*), alpine blueberry (*V. uliginosum* subsp. *alpinum*), *Sibbaldia procumbens,* and several willows (*Salix* spp.). A single storm-beaten specimen of Sitka spruce (*Picea sitchensis*) was also present.

Species List

The nomenclature follows that of Hale (1969) for the lichens, Hultén (1968) for the vascular cryptogams and flowering plants, and a combination of Lawton (1971) and the personal communication of W. B. Schofield for the mosses. Voucher specimens have been deposited in the Herbarium of the University of Minnesota at St. Paul and are identified by the numbers contained within the list.

LICHENS

Cladonia cariosa (Ach.) Spreng. (L333,L340).
Cladonia chlorophaea (Flk.) Spreng. (L342).
Cladonia gracilis (L.) Willd. (L335).
Cladonia pyxidata (L.) Hoffm. (L332).
Leptogium hirsutum Sierk (L339).
Lobaria linita (Ach.) Rabh. (L334).
Nephroma bellum (Spreng.) Tuck. (L338).
Peltigera canina (L.) Willd. var. *rufescens* (Weiss) Mudd (L337).
Solorina crocea (L.) Ach. (L336).
Stereocaulon paschale (L.) Hoffm. (L341).

MOSSES

POLYTRICHACEAE
Polytrichum juniperinum Hedw. (GB26,27).
DICRANACEAE
Dicranoweisia crispula (Hedw.) Milde (GB16,17).
GRIMMIACEAE
Rhacomitrium canescens (Hedw.) Brid. var. *ericoides* (Hedw.) Hampe (GB41).
MNIACEAE
Plagiomnium insigne (Mitt.) Koponen (GB3,4).
AMBLYSTEGIACEAEffl
Drepanocladus uncinatus (Hedw.) Warnst. var. *uncinatus* (GB50).
BRACHYTHECIACEAE
Brachythecium asperrimum (C. Muell.) Sull. (GB30).
Brachythecium tromsoense (Kaur. *et* Arn.) Limpr. (GB66).

VASCULAR CRYPTOGAMS AND FLOWERING PLANTS

CRYPTOGAMMACEAE
Cryptogramma crispa (L.) R. Br. var. *sitchensis* (Rupr.) Christens. (591).
ATHYRIACEAE
Cystopteris fragilis (L.) Bernh. subsp. *fragilis* (597).

ASPIDIACEAE
Polystichum lonchitis (L.) Roth (574).
PINACEAE
Picea sitchensis (Bong.) Carr. 584).
GRAMINEAE
Festuca altaica Trin. (529).
Phleum commutatum Gandoger var. *americanum* (Fourn.) Hult. (538).
Poa alpigena (E. Fries) Lindm. (528).
Trisetum spicatum (L.) Richter subsp. *alaskanum* (Nash) Hult. (531).
Trisetum spicatum (L.) Richter subsp. *spicatum* (535).
Vahlodea atropurpurea (Wahlenb.) E. Fries subsp. *latifolia* (Hook.) Pors. (533,537).
CYPERACEAE
Carex bicolor All. (550).
Carex macrochaeta C.A. Mey. (546).
Carex mertensii Prescott (548).
Carex pyrenaica Wahlenb. subsp. *micropoda* (C.A. Mey.) Hult. (547,549).
JUNCACEAE
Juncus drummondii E. Mey. (545).
Luzula parviflora (Ehrh.). Desv. (530,534).
LILIACEAE
Veratrum viride Ait. subsp. *eschscholtzii* (Gray) Löve & Löve (526).
SALICACEAE
Salix arbusculoides Anderss. (557).
Salix arctica Pall. subsp. *torulosa* (Trautv.) Hult. (553,556).
Salix barclayi Anderss. (552).
Salix reticulata L. subsp. *reticulata* (555).
Salix rotundifolia Trautv. (554).
Salix sitchensis Sanson (551).
CARYOPHYLLACEAE
Silene acaulis L. subsp. *acaulis* (589).
Stellaria monantha Hult. (572).
Stellaria sitchana Steud. (573).
RANUNCULACEAE
Aconitum delphinifolium DC. subsp. *delphinifolium* (585).
Aquilegia formosa Fisch. (577).
Ranunculus eschscholtzii Schlecht. (576).
Ranunculus occidentalis Nutt. subsp. *occidentalis* var. *brevistylis* Greene (575).
CRUCIFERAE
Cardamine umbellata Greene (582).
SAXIFRAGACEAE
Parnassia fimbriata Konig (543).
Parnassia palustris L. subsp. *neogaea* (Fern.) Hult. (544).
Saxifraga punctata L. subsp. *pacifica* Hult. (590a).
ROSACEAE
Geum aleppicum Jacq. subsp. *strictum* (Ait.) Clausen (586).
Geum macrophyllum Willd. subsp. *macrophyllum* (527).
Luetkea pectinata (Purch) Ktze. (593,594,595).
Sanguisorba stipulata Raf. (592).
Sibbaldia procumbens L. (590b).
LEGUMINOSAE
Astragalus alpinus L. subsp. *alpinus* (570).
Astragalus umbellatus Bunge (569).
Lupinus nootkatensis Donn (571).
VIOLACEAE
Viola langsdorffii Fisch. (580).
ONAGRACEAE
Epilobium adenocaulon Haussk. (541).
Epilobium angustifolium L. (588)
Epilobium hornemannii Rchb. (540).
UMBELLIFERAE
Heracleum lanatum Michx. (578).
Osmorhiza purpurea (Coult. & Rose) Suksd. (579).
ERICACEAE
Cassiope mertensiana (Bong.) D. Don (567).
Phyllodoce aleutica (Spreng.) Heller subsp. *glanduliflora* (Hook.) Hult. (568).
Vaccinium caespitosum Michx. (598).
Vaccinium uliginosum L. subsp. *alpinum* (Bigel.) Hult. (599,600).
PRIMULACEAE
Trientalis europaea L. subsp. *arctica* (Fisch.) Hult. (596).
SCROPHULARIACEAE
Veronica wormskjoldii Roem. & Schultfl. subsp. *alterniflora* (Fern.) Pennell (539,583,587).
Veronica wormskjoldii Roem. & Schult. subsp. *wormskjoldii* (542).

CAPRIFOLIACEAE
Sambucus racemosa L. subsp. *pubens* (Michx.) House var. *arborescens* Gray (581).
COMPOSITAE
Achillea borealis Bong. (560).
Agoseris glauca (Pursh) Raf. (566).
Antennaria isolepis Greene (565).
Arnica latifolia Bong. (563).
Arnica lessingii Greene subsp. *lessingii* (564).
Artemisia frigida Willd. (559).
Hieracium triste Willd. (561).
Senecio atropurpureus (Ledeb.) Fedtsch. subsp. *tomentosus* (Kjellm.) Hult. (562).
Solidago multiradiata Ait. var. *multiradiata* (558).

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Literature Cited

Billings, W. D. 1973. Arctic and alpine vegetation: similarities, differences, and susceptibility to disturbance. BioScience 23(12): 697-704.

Bohn, D. 1967. Glacier Bay. Sierra Club Press, San Francisco. 165 pp.

Bonham, C. D., and Ward, R. T. 1970. Phytosociological relationships in alpine tufted hairgrass (*Deschampsia caespitosa* (L.) Beauv.) meadows. Arct. Alp. Res. 2(4): 267-275.

Choate, C. M., and Habeck, J. R. 1967. Alpine plant communities at Logan Pass, Glacier National Park. Proc. Mont. Acad. Sci. 27: 36-54.

Cooper, W. S. 1931. The seed-plants and ferns of the Glacier Bay National Monument, Alaska. Bull. Torrey Bot. Club 57: 327-338.

————. 1939. Additions to the flora of the Glacier Bay National Monument, Alaska, 1935-1936. Bull. Torrey Bot. Club 66: 453-456.

————. 1942. An isolated colony of plants on a glacier-clad mountain. Bull. Torrey Bot. Club 69: 429-433.

Douglas, G. W. 1971. The alpine-subalpine flora of the North Cascade Range, Washington. Wasmann J. Biol. 29(2): 129-168.

Drury, W. H. 1962. Patterned ground and vegetation on southern Bylot Island, Northwest Territories, Canada. Contrib. Gray Herb. Harv. Univ. 190: 1-111.

Eckholm, E. P. 1975. The deterioration of mountain environments. Science 189: 764-770.

Hale, M. E. 1969. The Lichens. Wm. C. Brown Company Publishers, Dubuque. 226 pp.

Heusser, C. J. 1954a. Nunatak flora of the Juneau Ice Field. Bull. Torrey Bot. Club 81: 236-250.

————., Schuster, R. L., and Gilkey, A. K. 1954b. Geobotanical studies on the Taku Glacier anomaly. Geogr. Rev. 44(2): 224-239.

Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford. 1008 pp.

Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecol. Monogr. 32(2): 105-135.

Knapik, L. J., G. W. Scotter, and W. D. Pettapiece. 1973. Alpine soil and plant community relationships of the Sunshine area, Banff National Park. Arct. Alp. Res. 5(3): A161-A170.

Lawrence, D. B. 1977. Primary versus secondary succession at Glacier Bay National Monument, southeastern Alaska. *In* Proc. of the First Conference on Scientific Research in the National Parks, November 9-13, 1976, New Orleans.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan. 362 pp.

Lindsey, A. A. 1953. Notes on some plant communities in the northern Mackenzie Basin, Canada. Bot. Gaz. 115: 44-55.

Loewe, F. 1966. Climate, pp. 19-28. *In*: Soil Development and Ecological Succession in a Deglaciated Area of Muir Inlet, Southeast Alaska. Inst. Polar Studies, Rpt. #20. Ohio State Univ., Columbus. 167 pp.

Löve, D. 1970. Subarctic and subalpine: where and what? Arct. Alp. Res. 2(1): 63-73.

Muir, J. 1915. Travels in Alaska. Houghton Mifflin Co., Cambridge. 327 pp.

Noble, M. G., and C. D. Sandgren. 1976. A floristic survey of Muir Point, Glacier Bay National Monument, Alaska. Bull. Torrey Bot. Club 103(3): 132-136.

Price, L. W. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic alpine tundra. Ecology 52(4): 638-647.

Streveler, G. P., and B. B. Paige. 1971. The Natural History of Glacier Bay National Monument, Alaska. National Park Service, Glacier Bay National Monument, Alaska. 89 pp.

————., I. A. Worley, C. J. Terry, and R. J. Gordon. 1973. Dixon Harbor Biological Survey. National Park Service, Glacier Bay National Monument, Alaska. 241 pp.

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Inferred Holocene Temperature Changes in the North Coast Ranges of California*

Abstract

The remains of fish scales from two sediment cores taken in Clear Lake, California, have been used to estimate the sizes of fish at various points in time over the last ~12,000 years. Since growth rates of fish are primarily temperature-dependent, their patterns of growth constitute a valuable climatic response record reflecting variations in temperature.

Introduction

The patterns of growth reconstructed from fish scales may provide sensitive climatic response records, indicating fluctuations in temperature. Fish are poikilotherms and their metabolic rates vary positively with the temperature of their environment. Their vital processes are generally accelerated by warmer temperatures and decelerated by cooler ones (Alexander, 1967; Lagler *et al.*, 1962). In temperate regions fish also undergo seasonal fluctuations in growth rates. These seasonal pulses in growth are recorded in bones and scales as annuli (Chugunova, 1959; Ovchynnyk, 1962; McKern *et al.*, 1974) (Fig. 1). Appropriate fish remains can be used to identify type of fish, to reconstruct its size at the end of each year of growth, and, in situations in which data are available for a long period of time, to infer changes in temperature.

Methods

This method was first applied to the materials recovered from a series of eight sediment cores taken from Clear Lake, California, by the U.S. Geological Survey (Sims, 1974). Fish remains from two of these cores have been analyzed. The two cores (numbers 6 and 7) are from the Oaks and Highlands Arms of Clear Lake, respectively (Figure 2). The total number of scale remains from the samples of these two cores is 1580. All scales were mounted in glycerine jelly and identified. From this total approximately 85 percent were identified as belonging to *Hysterocarpus traski* Gibbons (Tule perch), an embiotocid native to Clear Lake (Hopkirk, 1974; Casteel, 1972). The scales of this species were then examined to determine which showed adequate annuli for growth reconstructions. A total of 255 Tule perch scales from both cores were found to be suitable. The annuli were identified on these scales and measurements of the antero-lateral

*Publication approved by the Director, U.S. Geological Survey.

radius from the nucleus to each annulus were made (Fig. 1). The standard lengths (in mm) of the fish at each annulus or year of growth were determined from these radial measurements using the regression of standard length on scale radius established from recent specimens of this species. Details of these procedures as well as the basic data have been presented elsewhere (Casteel *et al.*, 1975, 1977, 1977).

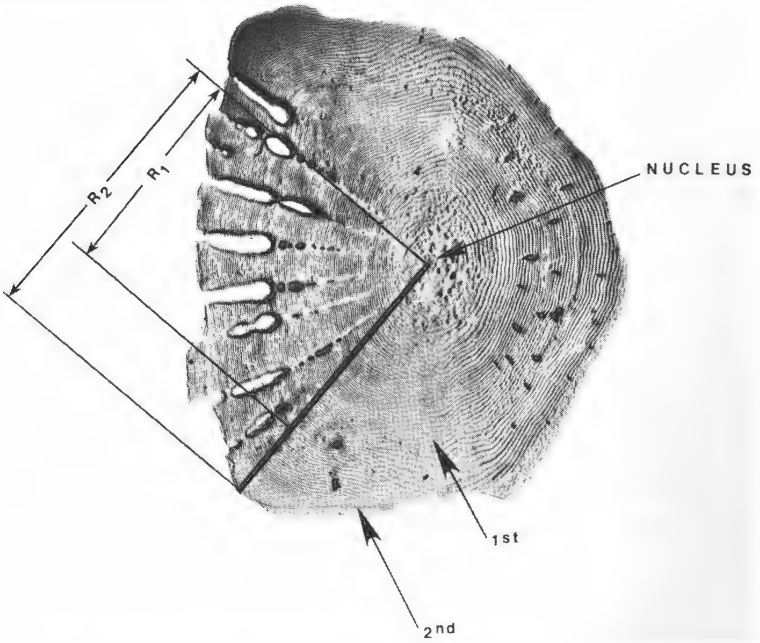

Figure 1. Scale of *Hysterocarpus traski* Gibbons (Specimen 136-13) from Core 7 showing measurement of antero-lateral radius to first (R_1) and second (R_2) annuli (x20). Anterior field of scale is to the viewer's left.

Results

Analysis of the fish scales from Core 7 indicated a period of depressed temperatures between ~9000 and 10,000 BP followed by a relatively steady increase in temperature which peaked between ~4000 and 2800 BP. The data indicated a period of decreasing temperature since ~2800 BP (Casteel *et al.*, 1977). The data from Core 6 indicated the same pattern of temperature change over the last ~11,000 years. Results for the last 3000 years, however, differed between age class 1 and age classes 2 and 3. The former indicated a period of increasing temperature since ~1800 BP, whereas the latter indicated rising temperatures between ~3000 and 1800 BP, followed by a steady and marked decline in temperature (Casteel *et al.*, 1977).

Under the assumption that the records from these cores should be responding to the same general climatic influences of increasing or decreasing temperature, the results of the two independent studies have been combined. The mean standard lengths for each slug from Cores 6 and 7 were plotted against the mean ages for these slugs as determined from estimates of the rates of sedimentation in the relevant Holocene parts of each core. The data were partitioned according to age classes. Only the data for age classes 1 through 3 were examined because those for age classes 4 through 6 were based upon extremely small sample sizes and highly subject to random variations. Since these

Figure 2. Map of Clear Lake, California, study area showing locations of Cores 6 and 7 in the Oaks and Highlands Arms, respectively.

latter age classes constitute only 9 percent of the available data, their exclusion was believed to be justified.

Figure 3 illustrates the result of combining the data from Cores 6 and 7. The general pattern is one of increasing temperature in the North Coast Ranges from ~12,000 to 3000 BP, followed by a general decline in temperature toward the present. Although this pattern is probably least apparent in age class 1 (Fig. 3A), a runs test indicates a significant time trend in the data ($\alpha = .05$) (Siegel, 1956). The mean standard lengths for all three age classes were tested against their representative averages for the entire ~12,000-year period using a χ^2 test and all were found to show significant non-random patterning ($\alpha < .01$).

Discussion and Conclusions

Data for age class 3 probably reflect best the climatic or temperature response record. Here temperature is increasing between ~12,000 and 8000 BP. This period is followed by a period of decreasing temperatures lasting until ~5000 BP. Temperatures then begin to rise to their Holocene zenith between ~5000 and 3000 BP, after which they decline toward the present.

While these results diverge somewhat from the general model of post-Pleistocene temperature/precipitation change for western North America (Antevs, 1952, 1955; Bryan and Gruhn, 1964), they match relatively well with more recent data concerning the termination of the Altithermal and marked cooling since 1000 BP as determined

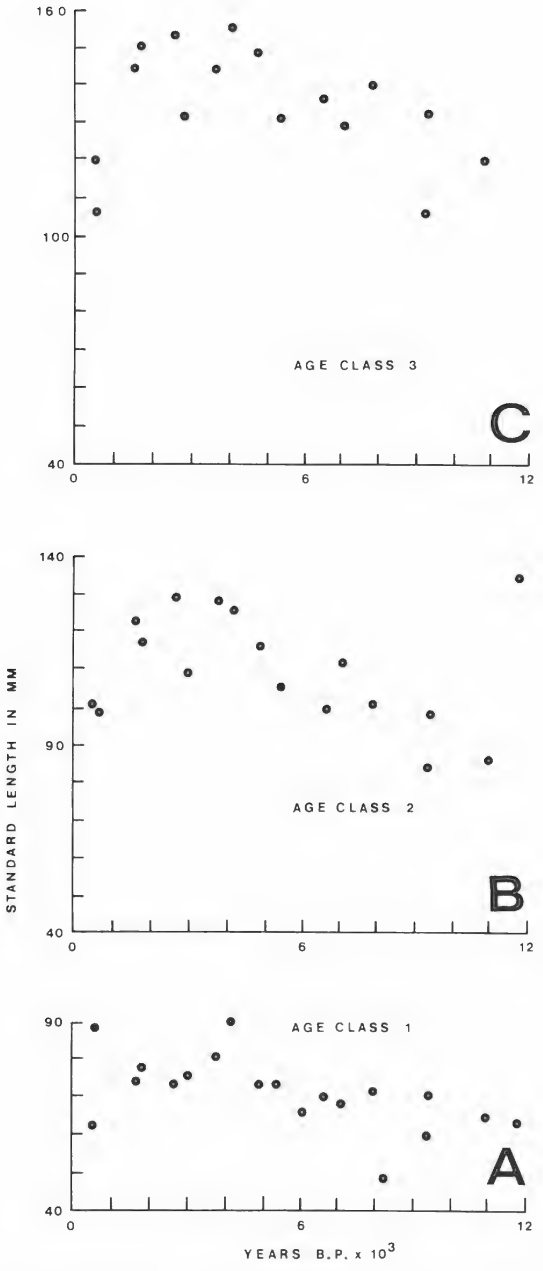

Figure 3. Estimated size (standard length in mm) of *Hysterocarpus traski* Gibbons. Ordinate, estimated mean standard lengths in mm; abscissa, mean age of samples in ^{14}C years BP. A, age class 1; B, age class 2; C, age class 3. Temperature change during this period is inferred to have followed a similar pattern.

from studies of bristlecone pine in the White Mountains of California (LaMarche, 1973, 1974), as well as in Nevada (LaMarche and Mooney, 1967). The results are consistent with those of Adam (1967) and Heusser (1960) and with estimates of the onset of Neoglacial conditions in the Sierra Nevada and California generally by Porter and Denton (1967). Generally, the time period from 2510 to 2760 BP has been seen as a time of increased precipitation and/or decreased evaporation in the Northern hemisphere and a major warming change is said to have occurred between 4230 and 4240 BP (Wendland and Bryson, 1974). These same authors also argue for a probable climatic change between 5900 and 6050 BP (Wendland and Bryson, 1974; Denton and Karlén, 1973). This finding coincides with the period of mid-Holocene temperature depression indicated in Figure 3.

Finally, a recent study of Holocene changes in the water level of Lower Klamath Lake, located approximately 320 km north-northeast of Clear Lake, has indicated periods of high lake levels at 4200 to 6000 BP and 600 to 1000 BP, with low lake levels between 1000 and 4200 BP (Grayson, 1967a,b). These periods of high lake stands coincide very well with periods of decreased temperature indicated in Figure 3. This relationship is also true for the mid-Holocene period of low lake level and the high temperatures indicated in Figure 3. Such an inverse relationship between temperature and precipitation is characteristic of the Köppen-Geiger Csb climates with marked summer/dry and winter/wet seasons (Strahler, 1965; Trewartha *et al.*, 1967). This same pattern was earlier proposed by Martin (1963) with regard to increased Altithermal aridity in California.

These results indicate that the use of fish scales may well provide a further means of inferring temperature changes, thus allowing for a discussion of Holocene temperature change without the need to consider both temperature and atmospheric moisture simultaneously (Deevey and Flint, 1957).

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Literature Cited

Adam, D. P. 1967. Late-Pleistocene and recent palynology in the central Sierra Nevada, California. Pp. 275-301 *In* E. J. Cushing and H. E. Wright, Jr. (eds.), Quaternary Paleoecology. Yale University Press. New Haven. 433 pp.

Alexander, R. McN. 1967. Functional Design in Fishes. Hutchinson. London. 160 pp.

Antevs, E. 1952. Climatic history and the antiquity of man in California. University of California Archaeological Survey, Report 16: 23-31.

————. 1955. Geologic-climatic dating in the west. Amer. Antiq. 29: 307-315.

Bryan, A. L., and R. Gruhn. 1964. Problems relating to the Neothermal climatic sequence. Amer. Antiq. 29: 307-315.

Casteel, R. W. 1972. A key, based on scales, to the families of native California freshwater fishes. Proc. Calif. Acad. Sci. 39: 75-86.

————, D. P. Adam, and J. D. Sims. 1975. Fish remains from Core 7, Clear Lake, Lake County, California. U.S. Geol. Surv., Open File Rep. No. 75-173.

————, ————, and ————. 1977. Late Pleistocene and Holocene remains of *Hysterocarpus traski* (Tule perch) from Clear Lake, California, and inferred Holocene temperature fluctuations. Quat. Res. 7: 133-143.

————, C. K. Beaver, D. P. Adam, and J. D. Sims. 1977. Fish remains from Core 6, Clear Lake, Lake County, California. U.S. Geol. Surv., Open File Rep. No. 77-639.
Chugunova, N. I. 1959. Age and Growth Studies in Fish: A Systematic Guide for Ichthyologists. Akademiia Nauk. SSSR. Moscow. 132 pp.
Deevey, E. S., and R. F. Flint. 1957. Postglacial hypsithermal interval. Science 125: 182-184.
Denton, G. H., and W. Karlén. 1973. Holocene climatic variations—their pattern and possible cause. Quat. Res. 3: 155-205.
Grayson, D. K. 1976a. A note on the prehistoric avifauna of the Lower Klamath basin. The Auk 93: 830-833.
————. 1976b. The Nightfire Island avifauna and the altithermal. Nevada Archaeological Survey, Research Paper No. 8: 74-102.
Heusser, C. J. 1960. Late-Pleistocene environments of north Pacific North America. Amer. Geog. Soc., Spec. Publ. No. 35.
Hopkirk, J. D. 1974. Endemism in Fishes of the Clear Lake Region of Central California. Univ. Calif. Publ. Zool. 96.
Lagler, K. F., J. E. Bardach, and R. R. Miller. 1962. Ichthyology. Wiley. New York. 545 pp.
LaMarche, V. C., Jr. 1973. Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. Quat. Res. 3: 632-660.
————, 1974. Paleoclimatic inferences from long tree-ring records. Science 183 1043-1048.
————, and H. A. Mooney. 1967. Altithermal timberline advance in the western United States. Nature 213: 980-982.
Martin, P. S. 1963. The Last 10,000 Years. Univ. Ariz. Press. Tucson. 87 pp.
McKern, J. L., H. F. Horton, and K. V. Koski. 1974. Development of steelhead trout (*Salmo gairdnerii*) otoliths and their use for age analysis and for separating summer from winter races and wild from hatchery stocks. J. Fish. Res. Bd. Canada 31: 1420-1426.
Ovchynnyk, M. M. 1962. The use of scales and bones for age determination of the Great Lakes whitefish *Coregonus clupeaformis clupeaformis* (Mitchill). Zool. Anz. 169: 198-217.
Porter, S. C., and G. H. Denton. 1967. Chronology of neoglaciation in the North American cordillera. Am. J. Sci. 265: 177-210.
Siegel, S. 1956. Nonparametric Statistics. McGraw-Hill. New York. 312 pp.
Sims, J. D. 1974. Searching for prehistoric earthquakes in lake sediments. Earthquake Information Bulletin 6: 3-9.
Strahler, A. N. 1965. Introduction to Physical Geography. Wiley. New York. 455 pp.
Trewartha, G. T., A. H. Robinson, and E. H. Hammond. 1967. Physical Elements of Geography. McGraw-Hill. New York. 527 pp.
Wendland, W. M., and R. A. Bryson. 1974. Dating climatic episodes of the Holocene. Quat. Res. 4: 9-24.

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The Occurrence of Neotenic Rough-skinned Newts (Taricha granulosa) in Montane Lakes of Southern Oregon

Abstract

Populations of neotenic rough-skinned newts (*Taricha granulosa*) were found in seven lakes and ponds at elevations from 1743 to 1847 m above sea level in the southern Cascade Mountains of Oregon. In localities where large numbers were observed, the proportion of salamanders retaining gills or gill stubs ranged from 87 to 100 percent. Climatic conditions in the study area are harsh, with long cold winters and dry summer seasons. By remaining in the more stable aquatic environment, salamanders can better survive the drastic climatic changes. *T. granulosa* in the study area are probably facultative in their ability to metamorphose, since they are found occasionally without gills, and gill tissue is resorbed in the laboratory with and without exposure to thyroxin.

Introduction

The rough-skinned newt, *Taricha granulosa*, is found along the humid Pacific coast of North America, from Admiralty Island, Alaska, to Santa Cruz and Santa Clara Counties, California (Stebbins, 1951). In Oregon this species occurs primarily west of the crest of the Cascade Mountains, with isolated populations in eastern Oregon (Stebbins, 1951).

It is the most aquatic member of the genus *Taricha*, with some populations having aquatic individuals through most of the year (Pimentel, 1960; Riemer, 1958; Twitty, 1942). Previous investigators have described the occasional occurrence of neoteny in *T. granulosa*. Nussbaum and Brodie (1971) reported that occasional adults from Kittitas County, Washington, retained gill remnants. Riemer (1958) reported gill-bearing adults from San Mateo County, California, and from Latah County, Idaho. Bishop (1943) and Farner and Kezer (1953) described the presence of gill tissue in a number of *T. g. mazamae* from Crater Lake, Oregon.

This report describes the distribution and occurrence of neotenic *T. granulosa* from the southern Cascade Mountains of Oregon. A preliminary experiment on the effects of thyroxin on gill tissue is also described.

Methods and Materials

Study Area

Neotenic *Taricha* were found in lakes located within the Rogue River National Forest and Winema National Forest, Klamath and Jackson Counties, Oregon, at elevations from 1743 to 1847 m above sea level. These lakes form an almost linear sequence, from North Blue Lake in the south to North Lake in the Seven Lakes Basin in the northern part of the study area. This region lies within the southern portion of the Cascade Mountains, referred to as the High Cascades Province (Baldwin, 1964). It is an area of rolling terrain interrupted by glaciated channels carrying westward flowing streams. The area is geologically young, with volcanic peaks and cones rising from 5 to 1600 m above the surrounding terrain.

The climate is harsh in winter, with much snowfall and sub-freezing temperatures; the summer season is moderately warm but dry. Table 1 lists climatic data for nearby Crater Lake, which lies approximately 40 km north of the study area, and Fish Lake, located 15 km south of the study area.

TABLE 1. Climatic data from representative weather stations near the study area.

				PRECIPITATION (mm)			TEMPERATURE (°C)				
Station	Elevation	Latitude	Longitude	Annual Mean	June Through August Mean	Annual Snowfall Mean	Annual Mean	Jan. Mean Minimum	Jan. Mean	July Mean	July Mean Maximum
Crater Lake National Park Headquarters	1974m	42°54'	122°08'	1643	99	13,241	3.8	-3.7	-8.4	13.4	21.9
Fish Lake	1429	42°23'	122°21'	1113	75	4,361	6.7	-2.0	-7.3	16.2	25.6

Source: U.S. Weather Bureau (1956, 1965).

The dominant canopy tree species were red fir (*Abies magnifica*) and mountain hemlock (*Tsuga mertensiana*). Subdominant species included Western white pine (*Pinus monticola*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). Dominant shrub species included pine-mat manzanita (*Arctostaphylos nevadensis*), and grouse huckleberry (*Vaccinium scoparium*) (Callan and Lang, unpublished data). Forests of this composition may be considered "subalpine forest" within the upper part of Merriam's Canadian Life Zone or the lower part of the Hudsonian Life Zone (Franklin and Dyrness, 1969).

Taricha were observed and collected during July, August, and October of 1974 and August 1975.

Thyroxin experiment

Newts from Horseshoe Lake, Klamath County, Oregon, were maintained in white plastic containers containing 5 liters of aged tap water at 5 cm depth at an average temperature of 20 C from 17 October to 12 December 1974. Four salamanders (mean snout-vent length 39.7 mm) maintained in aged tap water acted as controls. Four other salamanders (mean snout-vent length 43.3 mm) were kept in a 1:500,000 thyroxin solution. Gill length on the right side were measured before and after treatment.

Results

Aquatic *T. granulosa* were collected from six of the seven lakes found to contain them; North Blue Lake, Horseshoe Lake, Carey Lake, Island Lake, unnamed pond north of Margurette Lake ("Margurette pond"), and North Lake (Table 2). No collections were made at South Lake. Where large numbers were collected, most newts were found to possess gills (Table 2) which were in various degrees of development. Most individuals had three pairs of gills, each consisting of a fairly stout central stem, or ramus, often bearing low rounded swellings or occasional respiratory processes (fimbriae) typical of larval *Taricha*. Remnants of the larval gill arches and gill rakers were evident in some individuals as folds of tissue ventrolateral to the rami. Only 18 percent of the *Taricha* sample from Horseshoe Lake retained these gill arch remnants, with population samples

TABLE 2. Lake descriptions and locations.

No.	Name	Legal Location Willamette Meridian	Elevation	Surface Area	Depth (Max)	Additional Data	Taricha Observed	Sample Size	Percent Neotenic
1.	North Blue Lake	T.35S., R.4E., Sec 13	1774m	2.8h	1.5m	pH=7.0 Some littoral vegetation	Yes	32	87%
2.	Unnamed shallow pond	T.35S., R.4E., Sec 13	1774	1.2	.9	pH=7.0 Boulders and logs. **Ambystoma macrodactylum**	No		
3.	Round Lake	T.35S., R.4E., Sec 13	1786	1.0	3.7	pH=6.9 Small amount of rubble and sandy gravel. Salmonid introduction. **Rana cascadae**	No		
4.	South Blue Lake	T.35S., R.5E., Sec 19	1719	3.6	10.1	pH=7.5 PO_4^-=.012, NO_3^-=0, alk=3.27* Boulders at foot of talus slope. Salmonid introduction	No		
5.	Horseshoe Lake	T.35S., R.5E., Sec 19	1743	8.1	3.7	pH=7.5 PO_4^-=.029 ppm, NO_3=trace, alk=11.25* Rocky shoal. Areas with littoral vegetation. Salmonid introduction. **R. cascadae, B. boreas, A. macrodactylum**	Yes	68	98%
6.	Pear Lake	T.35S., R.5E., Sec 19, 20	1756	10.1	7.0	pH=7.5 Small amount of rocky shoal, some littoral vegetation. Salmonid introduction. **R. cascadae**	No		
7.	Carey Lake	T.35S., R.5E., Sec 20	1765	2.0	9.5	pH=7.5 PO_4^-=0, NO_3^-=0, alk=12.34* Littoral vegetation, some rocky areas. Salmonid introduction, **R. cascadae, B. boreas**	Yes	6	50%
8.	Island Lake	T.35S., R.5E., Sec 16	1798	18.2	5.2	pH=7.2 Small rubble area. Some meadows, littoral vegetation. Salmonid introduction. **R. cascadae, B. boreas, H. regilla,** Leeches	Yes	1	0%
9.	Lake Notasha	T.34S., R.5E., Sec 35	1834	6.1	8.2	pH=7.0 Rocky shoal area, Salmonid introduction, **B. boreas**	No		
10.	Lake Elizabeth	T.34S., R.5E., Sec 35	1834	2.0	2.4	**B. boreas,** Salmonid introduction	No		
11.	Isherwood Lake	T.34S., R.5E., Sec 35	1829	14.2	5.2	Some rocky and sandy areas, Salmonid introduction, **B. boreas, R. cascadae, H. regilla**	No		
12.	Trappers Lake	T.34S., R.5E., Sec 23	1810	8.1	3.4	Fine rock and rubble shallow areas, littoral vegetation, Salmonid introduction, **R. cascadae**	No		
13.	Unnamed, South of Trappers Lake	T.34S., R.5E., Sec 23	1810	.4	.8	pH=6.5 Littoral sedges, **A. macrodactylum** larvae	No		

TABLE 2. Cont'd.

No.	Name	Legal Location	Elevation	Surface Area	Depth (Max)	Additional Data	Taricha Observed	Sample Size	Percent Neotenic
14.	Margurette Lake	T.34S., R.5E., Sec 23	1835	14.2	8.8	Large shallow sand and rubble shoal. Salmonid introduction, **R. cascadae**	No		
15.	Unnamed, North of Margurette ("Margurette Pond")	T.34S., R.5E., Sec 23	1835	.8	1.4	Emergent vegetation, rooted submerged plants	Yes	30	93%
16.	Donna Lake	T.34S., R.5E., Sec 23	1810	2.0	2.7	Some boulders, littoral vegetation, Salmonid introduction, **R. cascadae**	No		
17.	South Lake	T.33S., R.5E., Sec 34	1945	3.6	1.5	Shoal area, some littoral vegetation, **R. cascadae**	Yes	0	
18.	Middle Lake	T.33S., R.5E., Sec 34	1859	12.2	3.7	Small gravel shoal, submerged and emergent vegetation. **B. boreas, R. cascadae**	No		
19.	North Lake	T.33S., R.5E., Sec 34	1847	2.8	1.8	pH=7.5 Surrounded by meadows. Fine clay-detritus bottom. Some emergents and submerged plants. Salmonids introduced, none surviving; **R. cascadae B. boreas, A. macrodactylum,** Leeches **(Haemopis grandis)** *mg/1 as HCO_3^-	Yes	42	100%

Compiled from personal observations, Oregon State Game Commission Reports (1970, Wustenberg 1953, Heckart 1961) and U.S. Geological Survey maps.

from Carey Lake, North Blue Lake, Margurette pond, and North Lake retaining 33, 38, 60, and 86 percent, respectively. Due to the fragility of the skin tissue surrounding these folds, it was not always possible to determine if the slits were functional.

Immature newts with typical adult coloration and granular skin varied in minimum sizes from lake to lake, with an inclusive range of 70.3 to 108.5 mm total length (TL). Chandler (1918) reported immature transformed individuals of 58 to 135 mm TL collected at lower elevations. Adults, differentiated from juveniles in this study on the basis of convoluted oviducts in females and large discrete testes in males, ranged from 88.0 to 207.4 mm TL. On October 4, 1974, pairs in amplexus were observed at Horseshoe Lake. Large yolked eggs and large multi-lobed testes in specimens collected at this time suggest a late autumn egg-laying period which has been reported for other high elevation populations of *T. granulosa* (Chandler, 1918; Garber and Garber, 1978).

Table 2 describes the ponds and lakes investigated during the summers of 1974 and 1975. The surface area, depth, elevation, and location are listed, with additional information where available, including pH, associated vertebrate species, and other physical and biotic data. Vegetation was limited in most cases to areas of emergent sedges or small plants growing on the bottom. The lake substrates were primarily fine clay and detritus particles, with some areas of more firm sand and pebble shoals. The long-toed salamander (*Ambystoma macrodactylum*) was occasionally observed, along with the Western toad (*Bufo boreas*), the Pacific tree frog (*Hyla regilla*), and the Cascade frog (*Rana cascadae*). Most of the deeper lakes have been stocked with salmonids, primarily Eastern brook trout (*Salvelinus fontinalis*), and occasionally rainbow trout (*Salmo gairdnerii*).

In laboratory experiments concerning the effect of thyroxin on gill tissue, both control and treated salamanders resorbed gill tissue (Table 3).

TABLE 3. Effects of thyroxin on gill length in **Taricha granulosa** from Horseshoe Lake.

	Date	Control	Thyroxin
N		4	4
Mean	17 October	1.8	2.5
gill length (mm)	12 December	1.1	0.9

Conclusion

Neoteny, the retention of larval characteristics beyond the normal larval period, has evolved convergently in every family of salamanders. Several theories have been proposed to explain the basis of this condition. Associated with most neotenic populations of salamanders are factors including a stable aquatic environment surrounded by a hostile terrestrial environment (Brandon and Bremer, 1966; Carr and Goin, 1943; Dent, 1968; Nussbaum and Clothier, 1973; Tihen, 1942). Under these conditions it has been proposed that neoteny will evolve because of the adaptive advantage of remaining in the more stable aquatic environment (Sprules, 1974a, b; Wilbur and Collins, 1973). The ponds and lakes included in this study share the characteristics associated with previous studies of neotenic salamanders. Winter temperatures are below freezing, and snowfall is high; summer temperatures are moderate while rainfall is low (Table 1). Because of the climatic conditions, depth of the water bodies is important since this is one factor upon which the stability of the aquatic habitat is based. Shallow ponds are

unsuitable if they dry during the summer or freeze solid in the winter. One shallow pond in the study area (adjacent to North Blue Lake, maximum depth 0.9 m) was observed to have totally evaporated during October of 1974, and may do so during typically dry summer and fall seasons. An additional limiting factor to the existence of newts is the presence of fish. The lack or rarity of fish has been cited previously as probably important for aquatic salamander survival (Brandon and Bremer, 1966; Burger, 1950; Carr and Goin, 1943; Larson, 1968; Sprules, 1974a). Although *T. granulosa* has very poisonous skin secretions (Brodie, 1968), individuals have occasionally been found in the stomachs of fish (Chandler, 1918; Vincent, 1947). Nevertheless, predation may be greater on the larvae, which are considerably less noxious than the adults (E. D. Brodie, Jr., pers. comm.). In addition to predation, competitive interactions between fish and salamanders have also been suggested as the cause of elimination or reduction in numbers of salamanders (Evendon, 1948; Sprules, 1974a). Evidence in the present study implicating the importance of depth of water interacting with the presence of fish is given by the example of North Lake. With a maximum depth of 1.8 m, North Lake is apparently adequate for providing refuge for overwintering newts. All individuals examined were neotenic, and appeared to be quite abundant. However, this lake, apparently due to its relatively shallow depth, is not adequate for the winter survival of stocked salmonids (Oregon State Game Commission, 1970). Other factors, such as exposure, or amount of shallow shoal area, may also act upon the suitability of a pond for salamanders and/or fish.

The above arguments give indications of the limits for survival of montane populations of aquatic salamanders, but the question of why these salamanders retain larval characteristics is not answered. Any selective advantage of gill retention in *T. granulosa* is not presently known. Perhaps the respiratory function of the gills is advantageous. However, many of the gills examined were simple stubs, often with few or reduced respiratory processes. The retention of gills may be a "correlated response" (Mayr, 1963: 290) to selection for a totally aquatic condition. Thyroxin, in addition to being primarily responsible for the process of metamorphosis, is a "land drive" hormone in newts (Grant *et al.*, 1965). Hypofunction of the thyroid or loss of tissue sensitivity to thyroxin may be the basis for the retention of both the larval morphology (gills) and larval behavior (aquatic habitat preference). These alternatives may occur through genetic control or by exogenous factors. Some neotenic salamanders, termed facultative in their ability to metamorphose, usually have the genetic potential for metamorphosing under certain environmental conditions (Nussbaum and Clothier, 1973; Sprules, 1974a, b). The thyroid and/or pituitary is apparently marginally functional in these animals, and under certain conditions hypofunction will occur, resulting in neotenic forms (Porter, 1972: 371). Low temperature has been found to inhibit tissue response to thyroid horomone (Huxley, 1929; Snyder, 1956; Frieden, 1968) or the release of these hormones may be inhibited. An age threshold at which metamorphic tissue becomes less sensitive to thyroid hormones may also be involved (Lipchina, 1929). Individuals may pass through this period during the cold season when sensitivity to thyroxin is reduced (Snyder, 1956). Thus cold temperatures associated with high elevations may work in these ways to produce neotenic populations.

Starvation has been postulated as a possible cause of neoteny (Porter, 1972: 367). Newts at all study sites appeared healthy, and dissection revealed large fat bodies and

food in the gut in the majority of the samples. Therefore, lack of food is not the basis for neoteny in this study.

It has been suggested that, due to the need for iodine in the production of thyroid hormones, an environment lacking this element may be responsible for neoteny in amphibians. Since montane lakes and ponds generally contain little dissolved material, this fact may account for differences in the occurrence of neoteny between high and lower elevation populations (Porter, 1972: 372). Although metamorphosis has not been conclusively shown to be limited by the availability of iodine in any natural population, metamorphosis has been induced in neotenes by subcutaneous implantations of iodide crystals (Ingram, 1928) and by maintenance of salamanders in potassium iodide solution (Blair, 1961).

The proportion of gill-bearing adults in the salamander populations in this study was much higher than indicated for previously reported populations containing neotenes (Bishop, 1943; Farner and Kezer, 1953; Nussbaum and Brodie, 1971; Riemer, 1958). According to Bishop (1943), 15 percent of 26 *T. g. mazamae* retained gill vestiges. Fifty-one specimens (MXZ 67971-68021) from the same or nearby locality cited by Riemer (1958) in San Mateo County, California, were examined by me. Sixteen (31 percent) retained gill vestiges, but of a different form than observed in this study. Gill rami were not distinguished in these specimens, only dark-colored fimbriae being present.

Since *T. granulosa* from neotenic populations are occasionally found without gills, and since gill tissue is resorbed in the laboratory, the evidence thus far indicates a facultative ability for metamorphosis, at least for the single population studied in the laboratory. It is not known if individuals from any populations have evolved into permenent (paedogenic) larvae incapable of complete metamorphosis.

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Literature Cited

Baldwin, E. M. 1964. Geology of Oregon. Univ. Oregon Coop. Bookstore. Eugene. 165 pp.
Bishop, S. C. 1947. Handbook of Salamanders. The Salamanders of the United States, of Canada, and of Lower California. Ithaca, N.Y., Comstock. 555 pp.
Blair, A. P. 1961. Metamorphosis of *Pseudotriton palleucus* with iodine. Copeia 1961: 499.

Brandon, R. A., and D. J. Bremer. 1966. Neotenic newts, *Notophthalmus viridescens louisianensis*, in southern Illinois. Herpetologica 22: 213-217.
Brodie, E. D., Jr. 1968. Investigations on the skin toxin of the adult rough-skinned newt, *Taricha granulosa*. Copeia 1968: 307-313.
Burger, W. L. 1950. Novel aspects of the life history of two *Ambystomas*. J. Tennessee Acad. Sci. 25: 252-257.
Chandler, A. C. 1918. The western newt, or water-dog (*Notophthalmus torosus*), a natural enemy of mosquitoes. Oregon Agric. Coll. Exp. Sta., Bull. 152: 1-24.
Dent, J. N. 1968. Survey of Amphibian Metamorphosis, pp. 271-311 *in* Metamorphosis (W. Etkin and L. I. Gilbert, eds.) Appleton-Century-Crofts, New York. 459 pp.
Evendon, F. G. 1948. Food habits of *Triturus granulosus* in western Oregon. Copeia 1948: 219-220.
Farner, D. S., and J. Kezer. 1953. Notes on the amphibians and the reptiles of Crater Lake National Park. Amer. Midl. Nat. 50: 448-462.
Franklin, J. F., and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. U.S.D.A. For. Serv. Res. Pap. PNW-80.
Frieden, E. 1968. Biochemistry of amphibian metamorphosis, pp. 349-398 *in* Metamorphosis (W. Etkin and L. I. Gilbert, eds.) Appleton-Century-Crofts, New York. 459 pp.
Garber, D. P., and C. E. Garber. 1978. A variant form of *Taricha granulosa* (Amphiba, Urodela, Salamandridae) from northwestern California. J. Herp. 12:59-64.
Grant, J. R., W. C. Cooper, and G. Cooper, IV. 1965. Behavioral and integumentary changes associated with induced metamorphosis in *Diemyctylus*. Biol. Bull. 129: 510.
Heckart, L. 1961. Lake Survey of Some Lakes in the Rogue River, Deschuttes, and Willamette National Forests, 1960. Oregon State Game Commission Report, Bend, Oregon. 278 pp.
Huxley, J. S. 1929. Thyroid and temperature in cold blooded vertebrates. Nature 123: 712.
Ingram, W. R. 1928. Metamorphosis of the Colorado axolotl by injection of inorganic iodine. Proc. Soc. Exp. Biol. Med. 26: 191.
Larson, D. W. 1968. The occurrence of neotenic salamanders, *Ambystoma tigrinum diaboli* Dunn, in Devils Lake, North Dakota. Copeia 1968: 620-621.
Lipchina, L. P. 1929. The dependence of the process of metamorphosis in axolotls on factors of age, coloring, and sex. Zh. Eksp. Biol. Med. 13: 73-78.
Mayr, E. 1963. Animal Species and Evolution. Belknap Press, Cambridge. 797 pp.
Nussbaum, R. A., and E. D. Brodie, Jr. 1971. The taxonomic status of the rough-skinned newt, *Taricha granulosa* (Skilton) in the Rocky Mountains. Herpetologica 27: 260-270.
————, and G. W. Clothier. 1973. Population structure, growth, and size of larval *Dicamptodon ensatus* (Eschscholtz). Northw. Sci. 47: 218-27.
Oregon State Game Commission. 1970. Natural Lake, Reservoir, and Pond Habitat Inventory. Portland, unpublished data.
Pimentel, R. A. 1960. Inter- and intrahabitat movements of the rough-skinned newt, *Taricha torosa granulosa* (Skilton). Amer. Midl. Nat. 63: 470-496.
Porter, K. R. 1972. Herpetology. Saunders, Philadelphia. 534 pp.
Riemer, W. J. 1958. Variation and systematic relationships within the salamander genus *Taricha*. Univ. California Publ. Zool. 56: 301-390.
Snyder, R. C. 1956. Comparative features of the life histories of *Ambystoma gracile* (Baird) from populations at low and high altitudes. Copeia 1956: 41-50.
Sprules, W. G. 1974a. The adaptive significance of paedogenesis in North American species of *Ambystoma* (Amphibia: Caudata): an hypothesis. Canadian J. Zool. 52: 393-400.
————. 1974b. Environmental factors and the incidence of neoteny in *Ambystoma gracile* (Baird) (Amphibia: Caudata). Canadian J. Zool. 52: 1545-1552.
Stebbins, R. C. 1951. Amphibians of Western North America. Univ. California Press, Berkeley. 539 pp.
Tihen, J. A. 1942. A colony of fossil neotenic *A. tigrinum*. Univ. Kansas Sci. Bull. 28: 189-198.
Twitty, V. C. 1942. The species of California *Triturus*. Copeia 1942: 65-76.
U.S. Weather Bureau. 1956. Climatic summary of the United States—supplement for 1931 through 1952, Oregon. Climatography of the United States 11-13. 46 pp.
————. 1965. Climatic summary of the United States—supplement for 1951 through 1960, Oregon. Climatography of the United States 86-31. 96 pp.
Vincent, W. S. 1947. A checklist of amphibians and reptiles of Crater Lake National Park. Crater Lake National Park Nature Notes 13: 19-22.
Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science 182: 1305-1314.
Wustenberg, D. W. 1953. Lake Survey of Some Lakes in the Deschuttes, Willamette, and Rogue River National Forests. State of Oregon Game Commission Report. Portland, SOGC. 362 pp.

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Sherman Glacier Vegetation

Abstract

In 1976 thirty-two plant species were found growing on the debris deposited by a 1964 landslide onto the Sherman Glacier in southcentral Alaska. Many species characteristic of subalpine and alpine zones were found attached to thick clumps of sod which the landslide transported intact from adjacent hillsides. This finding illustrates the potential importance of landslides as dispersing agents.

Introduction

The development of a covering of debris on a glacier surface provides the opportunity to study plant succession on an unstable moving substrate. Extensive areas of supraglacial debris will both alter the regime of the glacier and ameliorate the climate for vegetation development. A reconnaissance of the 1964 landslide debris on the Sherman Glacier in southcentral Alaska was conducted during the thirteenth growing season after the slide to ascertain the character and extent of the established vegetation. With helicopter support five sites were sampled on 2-3 July 1976. These sites extended from the snowline near the upper center of the landslide (about 330 m above sea level at that time) down-glacier to a point just above the south side of the terminus (about 205 m above sea level).

Supraglacial Debris

An extensive covering of debris develops from either subglacial or supraglacial material. Downwasting of the glacier surface exposes and concentrates subglacial erosional material. This mechanism may produce ablation, medial, and terminal moraines. Alternatively, landslide, avalanche, and aeolian material may form a supraglacial debris covering. Such debris, if originally deposited in the ablation area, may never be covered by perennial snow or ice. If deposited farther up-glacier, however, this material will be buried by snow and ice and thus becomes subglacial debris which will eventually be reexposed by melting. Summer and autumn melting near the terminus may ultimately produce stagnant or detached ice covered by debris which is strongly altered by fluvial processes. Few glaciers display an extensive development of supraglacial debris and many display none.

Effect on Climate

A covering of debris, if large in extent, will cause changes in local climatic conditions. These changes may significantly alter the environment to which a vegetation cover will be exposed and so may influence the character and extent of developing vegetation.

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While few data are available, the meteorological observations on the Sherman Glacier landslide (Marangunić, 1972) illustrate some changes which occur. This landslide covers 8.5 km^2 of the ablation zone with rock debris averaging 1.3 m in thickness. On a clear day air flowing down-glacier is warmed 18 C while traveling over the debris (Marangunić, 1972). This temperature increase is caused by longwave thermal radiation from the landslide surface. Maximum temperatures near the landslide surface are often similar to those on hillsides flanking the glacier, but night temperatures often drop as low as those at locations on the ice. Temperatures at hillside locations rise more quickly than over the landslide but drop more rapidly over the landslide due to cool down-glacier winds. Supersaturation of the warm air over the landslide was found to occur when exposed to katabatic winds flowing down-glacier. These winds are produced by a cool-air layer about 20 m thick which flows down from the upper reaches of the glacier. Thus the conditions to which vegetation is subjected are similar to those on nearby hillsides but with large variations in thermal radiation and low night temperatures even during the growing season. Smaller areas of debris will cause less amelioration of the climate.

Supraglacial Vegetation

Factors which influence the character and extent of vegetation on debris-covered glaciers are the (1) nearby assemblages of plant species available for colonization; (2) climatic regime of the region as altered locally by the glacier and covering debris; (3) local wind directions and intensities (see Bonde, 1969); (4) location of the debris on the glacier; (5) stability of the debris; and (6) origin of the debris.

Figure 1. Ablation moraine on Childs Glacier with an extensively developed thicket of Sitka Alder (*Alnus crispa* [Ait.] Pursh subsp. *sinuata* [Regel] Hult.). The dark triangular area in the center of the photograph is exposed ice. Photograph taken on 3 July 1976.

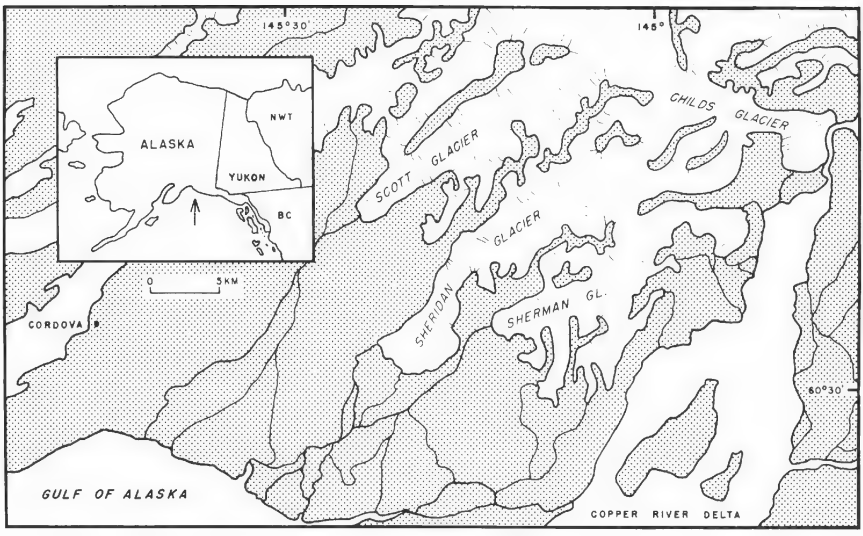

Figure 2. Map of the Sherman Glacier area.

Several of the glaciers which exhibit an extensive debris-mantle and which also support a covering of vegetation will be mentioned. The Red Glacier in the Chigmit Mountains along Cook Inlet (Post and LaChapelle, 1971) and the Childs Glacier (Figs. 1 and 2) in the Chugach Mountains of Alaska's southern coast support areas of dense vegetation on ablation moraine. The contorted medial moraines (as well as ablation moraine) bordering the terminus of the Malaspina Glacier near Yakutat Bay in southeastern Alaska support extensive forests with some Sitka spruce (*Picea sitchensis* [Bong.] Carr.) up to 160 years of age. Inward from the ice margin are found increasingly younger plant assemblages (Sharp, 1958). The influence of the location, stability, and origin of supraglacial debris will be illustrated with a discussion of the vegetation which is developing on the Sherman Glacier landslide.

The Sherman Glacier Landslide

On 27 March 1964, a strong earthquake (8.4 to 8.6 on the Richter scale then in use) released several rock avalanches onto the Sherman Glacier. The largest emanated from Shattered Peak and covered 8.5 km^2 of the lower reaches of Sherman Glacier and one of its tributaries (Figs. 2 and 3). The avalanche slid up to 5.3 km on a layer of compressed air and the highly unstable surface consists primarily of sharply angular sandstone boulders (Shreve, 1968). In 1965 Shreve (1968) noticed lichens, mosses, grasses, and sod which had been removed from adjacent hillsides and deposited on the landslide surface. In addition, large debris cones apparently traveled intact from the slopes of Shattered Peak to the landslide surface (Marangunić, 1972).

The Landslide Vegetation

There is virtually no vegetation in the upper portions of the landslide because the long persistence of snow results in an extremely short growing season. Even nearby hillsides

Figure 3. Sherman Glacier terminus on 2 July 1976. Landslide debris has reached the southern side of the terminus shown on the right side of the photograph. Shattered Peak, the source of the landslide debris, is the cloud-enveloped summit second from the left edge of the photograph.

at higher elevations have a much longer growing season due to thermal radiation from the vegetation and lack of similar cool down-glacier winds. The number of plant species observed increased down-glacier from two species at the highest location to nineteen species near the terminus. As the upper portion of the slide is rafted down-glacier into areas which are snow-free longer, vegetation will become established. Even near the terminus, where most of the vegetation occurs, individual plants are highly scattered (Fig. 4). Local slumping produced by ice-melt often uproots and buries plants and is most common near the terminus.

I found 32 recognizably distinct plant taxa belonging to 27 genera and (exclusive of the lichens) 19 families. Of these 32 species, 22 were attached to sod clumps, one was attached to undamaged sides of boulder fragments, and four probably survived the landslide by rooting from stem fragments. Four of the remaining five species have small, light seeds which were probably transported to the slide by strong winds. Bonde (1969) has shown that many plant disseminules are wind-deposited onto supraglacial debris despite the lack of special adaptations for dispersal by wind. Apparently even the relatively heavy seeds of the fifth species, Nootka lupine (*Lupinus nootkatensis* Donn), may be dispersed by especially strong winds. Ridley (1930) even considered the complete pods or separate valves with attached seeds to be easily wind-borne. The Nootka lupine seeds may also be dispersed by ptarmigan and other birds. The thick mats of organic material to which 22 species were attached could only have developed over a long period of substrate stability. Because many of these species are characteristic of nearby sub-

Figure 4. The surface of the Sherman Glacier landslide on 3 July 1976. Paul Cunningham, helicopter pilot, provides a scale beside a typical Sitka alder specimen.

alpine meadows and alpine tundras and are seldom or never encountered on new physiographic surfaces, they probably did not become established on the sod clumps after the landslide. Thus, much of the present vegetation is an expression of those species able to regenerate and flourish in this austere habitat after fortuitously landing at the surface of the debris.

In the list that follows a note indicates whether the specimen collected was attached to a clump of landslide-deposited sod or has apparently become established since the slide. The collections made at the three lowest locations visited account for 93 percent of the species encountered. Based upon that and the nature and extent of the slide, I would estimate that if the entire slide were sampled approximately ten more species might be found. The nomenclature follows Hale (1969) for the lichens, Lawton (1971) for the mosses, and Hultén (1968) for the vascular cryptogams and flowering plants.

List of Landslide Plants

LICHENS

Stereocaulon paschale (L.) Hoffm. (664) Survived landslide, interwoven with mosses attached to sod, occasional.

Thamnolia subuliformis (Ehrh.) Culb. (665) Survived landslide, interwoven with mosses attached to sod, occasional.

MOSSES

POLYTRICHACEAE

Pogonatum alpinum (Hedw.) Roehl. (669a) Survived landslide, attached to sod, common.

Pogonatum urnigerum (Hedw.) P. Beauv. (669b) Survived landslide, attached to sod, occasional.

DITRICHACEAE

Ceratodon purpureus (Hedw.) Brid. (669c) Survived landslide, attached to sod, common.

DICRANACEAE

Dicranum scoparium Hedw. (668b,670b) Survived landslide, attached to sod, common.

GRIMMIACEAE
Rhacomitrium canescens (Hedw.) Brid. (666,669d,670a) Survived landslide, attached to rock, common.

AMBLYSTEGIACEAE
Pleurozium schreberi (Brid.) Mitt. (668c,670c) Survived landslide, attached to sod, common.

RHYTIDIACEAE
Rhytidiadelphus loreus (Hedw.) Warnst. (667,668a) Survived landslide, attached to sod, common.

VASCULAR CRYPTOGAMS AND FLOWERING PLANTS

CRYPTOGRAMMACEAE
Cryptogramma crispa (L.) R. Br. var. *sitchensis* (Rupr.) Christens. (675) Survived landslide, attached to thick sod clumps, produced fertile fronds in both 1975 and 1976, several robust patches observed.

GRAMINEAE
Calamagrostis canadensis (Michx.) Beauv. (692) Survived landslide, attached to sod, flowered in 1975, occasional.
Trisetum spicatum (L.) Richter (693) Survived landslide, attached to sod, flowered in both 1975 and 1976, occasional.

CYPERACEAE
Carex macrochaeta C. A. Mey. (686,687,688) Survived landslide, attached to sod, many specimens in flower, second most common plant on landslide.

JUNCACEAE
Luzula parviflora (Ehrh.) Desv. (691) Survived landslide, attached to sod, in flower, occasional.
Luzula wahlenbergii Rupr. subsp. *piperi* (Cov.) Hult. (690) Survived landslide, attached to thick sod clumps, in flower, occasional.

SALICACEAE
Populus balsamifera L. (685) Probably survived landslide by rooting from stem fragments, generally less than 0.5 m high, no seedlings observed, none in flower, rare.
Salix barclayi Andersss. (683) Probably survived landslide by rooting from stem fragments, generally less than 0.7 m high, no seedlings observed, occasional individual in flower, common.
Salix sitchensis Sanson (684) Probably survived landslide by rooting from stem fragments, generally less than 0.6 m high, no seedlings observed, occasional individual in flower, common.

BETULACEAE
Alnus crispa (Ait.) Pursh subsp. *sinuata* (Regel) Hult. (671) Probably survived landslide by rooting from stem fragments, generally 0.75 to 1.75 m high, no seedlings observed, many specimens in fruit, by far the most common species on the slide.

CARYOPHYLLACEAE
Silene acaulis L. subsp. *acaulis* (677b) Survived landslide, attached to sod, rare.
Stellaria sitchana Steud. var. *bongardiana* (Fern.) Hult. (679,680) Established since slide, no sod attached, flowered in both 1975 and 1976, occasional.

SAXIFRAGACEAE
Heuchera glabra Willd. (676) Survived landslide, attached to sod, occasional.
Saxifraga caespitosa L. (677a) Survived landslide, attached to sod, occasional.
Saxifraga punctata L. subsp. *pacifica* Hult. (678) Established since slide, no sod attached, occasional.
Saxifraga sp. (689a) Established recently, no sod attached, depauperate, rare.

ROSACEAE
Geum calthifolium Menzies (674) Survived landslide, attached to thick sod clumps, flowered in both 1975 and 1976, several robust patches observed.
Luetkea pectinata (Pursh) Ktze. (677c) Survived landslide, attached to sod, in flower, observed only in upper portion of landslide, rare.
Sibbaldia procumbens L. (689b) Survived landslide, attached to sod, rare.

LEGUMINOSAE
Lupinus nootkatensis Donn (672) Established since the slide, no sod attached, flowered in 1975, leaves just emerging on 3 July 1976, observed only in lower portion of slide where it is common.

ONAGRACEAE
Epilobium latifolium L. (673,681,682) Established since the slide, no sod attached, none in flower, occasional.

SCROPHULARIACEAE
Veronica wormskjoldii Roem. & Schult. subsp. *wormskjoldii* (689a) Survived landslide, attached to sod, rare.

COMPOSITAE
Arnica lessingii Greene subsp. *lessingii* (689c) Survived landslide, attached to sod, occasional.

Conclusion

As the slide debris is rafted down-glacier a mantle of vegetation will continue to develop with some loss of individual plants where slumping occurs, especially near the terminus. Marangunić (1972) predicts several years of surging after the full debris edge reaches the terminus around 1985, and Bull (1969) predicts that the same behavior will occur between 1978 and 1980. The instability and thinning of debris during such activity will destroy much of the vegetation. Marangunić (1972) expects that debris-covered ice will become stagnant and separated from the glacier after the year 2000 and will slowly melt during the following 700 years.

It is anticipated that in the years ahead the largely landslide-deposited vegetation will be substantially augmented with early and mid-successional species. Eventually a vegetation cover may develop which is as extensive and diverse as that on the ice-cored moraines discussed by Post and Streveler (1976) at Lituya Bay in southeastern Alaska and studied by Birks (1977) on the Klutlan Glacier in the Yukon Territory. If no major advance occurs and if the ice beneath the Sherman Glacier landslide behaves and melts as predicted, it will be possible to observe the development of a complex mosaic of plant assemblages. It will be interesting to discover how long the present landslide-dispersed plants will persist as the character, extent, and structure of the vegetation changes.

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Literature Cited

Birks, H. J. B. 1977. The present flora and vegetation of the Klutlan Glacier, Yukon Territory, Canada: A study in plant succession. Manuscript in preparation.

Bonde, E. K. 1969. Plant disseminules in wind-blown debris from a glacier in Colorado. Arctic and Alpine Research 1: 135-139.

Bull, C. 1969. The 1978-1980 surge of the Sherman Glacier, south-central Alaska. Canadian Journal of Earth Sciences 6: 841-843.

Hale, M. E. 1969. The Lichens. Wm. C. Brown Co., Dubuque, Iowa. 226 pp.

Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, Calif. 1008 pp.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan. 362 pp.

Marangunić, C. 1972. Effects of a Landslide on Sherman Glacier, Alaska. Inst. Polar Studies Rep. No. 30. Ohio State University, Columbus, Ohio. 137 pp.

Post, A., and E. R. LaChapelle. 1971. Glacier Ice. University of Washington Press, Seattle, Washington. 110 pp.

————, and G. Streveler. 1976. The tilted forest: Glaciological-geologic implications of vegetated Neoglacial ice at Lituya Bay, Alaska. Quaternary Research 6: 111-117.

Ridley, H. N. 1930. The Dispersal of Plants throughout the World. L. Reeve & Co., Ashford, England. 744 pp.

Sharp, R. P. 1958. The latest major advance of Malaspina Glacier, Alaska. Geographical Review 48: 16-26.

Shreve, R. L. 1968. Sherman landslide. Pp. 395-401 *in*: The Great Alaska Earthquake of 1964 (Hydrology, Part A). Publ. 1603, Nat. Acad. Sci., Washington, D.C. 441 pp.

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Uptake of Mercury from Soils by Western Wheatgrass Seedlings[1]

Abstract

The uptake of mercury by western wheatgrass (*Agropyron smithii* cv. Rosana) seedlings from five eastern Montana soils amended with 1.0 ppm Hg applied as $Hg(NO_3)_2$ was investigated in a greenhouse study. Above-ground tissues showed plant/soil concentration factors of 0.01 to 0.1. Up to 21 percent of the soil-applied Hg was lost by volatilization during the 22-day growth period.

Introduction

With the development of the energy resources of the western United States have come concerns regarding the environmental impact of the emissions associated with power-generation on the grassland biome. Due to its volatility and known toxicity, mercury (Hg) emitted from both coal-fired and geothermal power plants has been a metallic airborne pollutant of particular concern.

Coal from the Powder River Basin of northeastern Wyoming and southeastern Montana contains an average of 0.09 ppm Hg (Swanson *et al.*, 1974). The scrubbers and electrostatic precipitators used to control air pollution from coal-fired power plants are ineffective in the removal of Hg, present in the hot flue gas primarily as metallic mercury vapor (Hg°), and about 90 percent of that in the coal is released to the environment (Billings and Matson, 1972; Montana State Department of Natural Resources and Conservation, 1974).

Numerous sites for the potential development of geothermally-powered electric generating plants exist in Oregon, California, Nevada, and New Mexico. Mercury present in geothermal reservoirs can be released to the surface environment with the live steam during drilling and venting, and from the spent steam in condensate ponds (U.S. Dept. of Interior, 1973; Siegel and Siegel, 1975).

Thus the potential for environmental contamination and bioconcentration of mercury exists in these energy development areas. Western wheatgrass (*Agropyron smithii*) is a widely distributed range species in the western United States and Canada, and is often the dominant species in the Northern Great Plains (Martin, 1969). Little is known regarding its uptake of heavy metals, a computerized search of Biological Abstracts since 1972 revealing only a single study (Munshower and Behan, 1971). The uptake of mercury from soils by western wheatgrass was therefore studied in a greenhouse experiment.

Methods and Materials

Five surface soils (Table 1) were collected from uncultivated sites in southeastern Montana, air-dried, and ground to pass a 2 mm sieve. The soil pH (1:2 soil:water), calcium

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TABLE 1. Chemical and physical properties of selected eastern Montana soils.

Soil Series	Classification	pH	$CaCO_3$ equiv. %	Organic C, %	Total N, %	Extractable P ppm	Extractable K ppm	Extractable Na meq/100g	Total Soluble Salts mmho/cm	Cation Exchange Capacity meq/100g	Total Hg µg/kg	Sand %	Silt %	Clay %
Arvada	Ustollic Natrargid, fine, montmorillonitic, mesic	8.1	0.08	1.6	0.10	3	526	0.87	0.43	22.2	60	35	25	40
Campspass	Typic Eutroboralf, fine, montmorillonitic	6.6	—	6.7	0.27	5	203	0.07	0.35	25.5	130	19	56	25
Heldt	Usteric Camborthid, fine, montmorillonitic, mesic	8.3	3.92	1.7	0.12	1	186	0.08	0.35	11.4	183	27	48	25
Bainville	Ustic Torriorthent, fine, silty, mixed (calcareous), mesic	7.5	0.04	1.0	0.08	2	231	0.07	0.28	15.8	73	29	42	29
Terry	Ustollic Haplargid, coarse-loamy, mixed, mesic	8.3	0.20	0.9	0.10	1	84	0.07	0.31	8.4	<60	74	14	12

carbonate equivalent, organic carbon (Walkley-Black titration), total Kjeldahl nitrogen, extractable P (0.5 *M* sodium bicarbonate, pH 8.5), total soluble salts (saturation extract electrical conductivity), extractable potassium and sodium, and cation exchange capacity (1*N* ammonium acetate, pH 7) were determined (Kauffman and Gardner, 1976). Native soil mercury levels were determined by flameless atomic absorption spectrometry following digestion of the soil with aqua regia. Particle size analysis was by the pipette method (Day, 1965). The ⅓-bar moisture percentage was determined by the method of the U.S. Salinity Laboratory Staff (1954).

The soils, in 70 g (oven-dry basis) portions, were amended with 1.0 μg Hg/g soil using ^{203}Hg-$Hg(NO_3)_2$ applied with sufficient water to reach the ⅓-bar content, and contained in plastic cups without drainage holes. There were 3 replicates per soil per treatment. After a 24-hour equilibration period, twenty seeds of "Rosana" western wheatgrass were applied to the surface of the soil and covered with 40 g of moist sand. The plants were grown in a chemical fume hood located in a greenhouse. Distilled water was added on alternate days to make up for evapotranspiration losses and to bring the soils back to the ⅓-bar moisture content. No fertility amendments were made to the soil either initially nor during the course of the experiment. Natural illumination was supplemented by incandescent lights (G.E. Gro-Sho; 16-hour-day length) whose heat was dissipated by a flowing-water filter cell. Twenty-two days after planting, the aboveground tissue was harvested, radioassayed using a NaI γ-scintillation spectrometer (Packard model 5230), and dried at 80 C. Tissue Hg concentrations were calculated from the specific activity of the added Hg assuming no dilution by the endogenous soil mercury pool.

In order to assess the extent of volatile loss of the added Hg from the soils during the course of plant growth, soil mercury content was monitored by radioassay of the entire soil mass using a small animal, whole-body, liquid scintillation spectrometer system (Armac model 446, Packard Instrument Co.). A special sample holder established a reproducible counting geometry in the sample well. The samples were counted using the 0.28 Mev γ-radiation of the ^{203}Hg after soil amendment and again after tissue harvest.

Results and Discussion

Plant/soil concentration factors ($CF = \frac{\mu g\ Hg/g\ tissue}{\mu g\ Hg/g\ soil}$) for Hg in the above ground portion of western wheatgrass seedlings range from 0.01 to 0.1 (Table 2). Tissue Hg concentrations were lowest for the Campspass and Arvada soils, the soils highest in organic matter and clay respectively, and highest in the high-lime Heldt soil. No toxicity

TABLE 2. Uptake of Hg by above ground portion of western wheatgrass seedlings grown for 22 days on soils amended with 1.0 μg Hg/g soil.
Tissue concentrations shown are means of 3 replicates ± standard error, and are calculated on a dry matter basis.

Soil Series	ng Hg/g DM
Arvada	31 ± 2.3
Campspass	12 ± 6.4
Heldt	96 ± 22
Bainville	40 ± 5.8
Terry	37 ± 8.3

symptoms or yield reductions with respect to control plants grown on unamended soils were evident. Tissue yields on the Arvada and Campspass soils were about double those on the Terry soil, with the Heldt and Bainville yields falling in the intermediate range.

The volatile loss of Hg, presumably as Hg°, from soils amended with divalent mercury has been reported by several investigators (Rogers, 1975; Hogg, 1976). At the end of the 22-day growth period, from 9 to 21 percent of the initially-applied mercury had been lost from the soil-plant systems (Table 3). As the above-ground portion of

TABLE 3. Percent of initially-added Hg remaining in soil (corrected for plant removal) at end of 22-day plant growth period.

Values reported are means of 3 replicates ± standard error.

Soil Series	% Hg remaining
Arvada	90.8 ± 0.4
Campspass	93.4 ± 0.2
Heldt	83.8 ± 0.2
Bainville	90.6 ± 0.5
Terry	79.4 ± 0.6

the seedlings are exposed to Hg vapors emanating from the soil, the Hg found in the aerial tissue is probably the result of both foliar interception of volatilized Hg (Zimmerman and Crocker, 1933), as well as translocation from the roots.

The concentration factors reported here are similar to those found for bromegrass (CF=0.05-0.06) grown for 49 days on soils amended with 10 μg Hg (as $HgCl_2$)/g soil (Hogg, 1976), and for wheat and barley (CF=0.04-0.11) grown to the heading-out or mature stage on soils amended with 0.5 μg Hg as $Hg(NO_3)_2$/g soil (Lee, 1974). Cadmium (Cd) is the Periodic Table neighbor of Hg in group IIb, and Munshower and Behan (1971) report a CF of 0.8 (based on acid extractable soil Cd) for western wheatgrass growing 20 miles from a zinc-cadmium smelter in Montana. Cd is generally considered to be more plant available than Hg (Lagerwerff, 1972).

In spite of the potential for both foliar and root uptake, only limited quantities of Hg were found in the above-ground portion of western wheatgrass grown on Hg-amended soils. Western wheatgrass would not appear to represent a source for food chain magnification of environmental mercury.

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Literature Cited

Billings, C. E., and W. R. Matson. 1972. Mercury emissions from coal combustion. Science 176: 1232-1233.

Day, P. R. 1965. Particle fractionation and particle size analysis. *In* C. A. Black (ed.) Methods of Soil Analysis. Agronomy 9:545-567. Am. Soc. of Agron., Madison, Wis. 1572 pp.

Hogg, T. J. 1976. The Fate of Applied Mercury in the Soil-plant System under Sewage Effluent Irrigation Conditions. University of Saskatchewan, Saskatoon, M.Sc. thesis. 111 pp.

Kauffman, M. D., and E. H. Gardner, 1976. Methods of Soil Analysis Used in the Soil Testing Laboratory at Oregon State University. Spec. Rept. 321, Or. Ag. Expt. Sta. 40 pp.

Lagerwerff, J. V. 1972. Lead, mercury and cadmium as environmental contaminants. Pp. 593-636, *in* J. J. Mortvedt, P. M. Giordano, and W. L. Lindsay (eds.) Micronutrients in Agriculture. Soil Science Society of America. Madison, Wis. 666 pp.

Lee, C. C. 1974. ^{203}Hg tracer studies on mercury uptake from soil by wheat and barley. Bull. Env. Contam. Toxic. 11:551-553.

Martin, N. L. 1969. Western Wheatgrass. Range plant leaflet 76, Cooperative Extension Service, Oregon State University. 1 p.
Montana State Department of Natural Resources and Conservation. 1974. Pp. 215-223, Draft environmental impact state on Colstrip electric generating units 3 and 4. Vol. 3A. 626 pp.
Munshower, F. F., and M. J. Behan. 1971. Ecological compartmentation of airborne cadmium in a grassland ecosystem (abstr.). Am. J. Bot. 58:476.
Rogers, R. D. 1975. Methylation of mercury in a terrestrial environment. Abstr. Int. Conf. on Heavy Metals in the Environment (Toronto, Canada) C-218.
Siegel, S. M., and B. Z. Siegel. 1975. Geothermal hazards. Mercury emission. Env. Sci. Tech. 9: 473-474.
Swanson, V. E., C. Huffman, Jr., and J. C. Hamilton. 1974. Composition and trace element content of coal, Northern Great Plains area. Pp. 52-83. U.S. Dept. Interior open file report, Northern Great Plains Resource Program, Mineral Resources Work Group Report (Feb. 1974).
U.S. Dept. of Interior. 1973. Final Environmental Statement for the Geothermal Leasing Program, v. 1, chapt. III, pp. 16-22. Washington, D.C. 92 pp.
U.S. Salinity Laboratory Staff. 1954. Methods for soil characterization. Pp. 83-126 *in* L. A. Richards (ed.) Diagnosis and Improvement of Saline and Alkali Soils. Agric. Handb. no. 60, USDA. U.S. Government Printing Office, Washington, D.C. 160 pp.
Zimmerman, P. W., and W. Crocker. 1933. The injurious effect of mercury vapor from bichloride of mercury in soil of rose houses. Boyce Thompson Inst. Profess. Papers 1 (no. 23):222-225.

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Habitat Preference and Dispersion of Nuttall's Cottontails[2]

Abstract

Dispersion in a population of Nuttall's cottontails (*Sylvilagus nuttallii*) was ascertained by live-trapping and by direct observation of individuals flushed along 32 transect lines across an 84.9-ha study area in central Oregon. Dispersion of 457 captures in three habitat types based on vegetative, edaphic, and topographic substrates was significantly different from a uniform distribution; however, dispersion of 86 cottontails flushed in the same habitats was not significantly different from a uniform distribution, but was significantly different from the distribution of captures. Observed differences in dispersion were believed to be related to diel activity patterns of cottontails, and to the physiographic and vegetative differences in habitats. Based on these conclusions, observed habitat preferences of cottontails on the study area were believed to be artifacts of the methods of quantification of dispersion of the population.

Introduction

This is a report of our attempts to determine habitat preferences of Nuttall's cottontails (*Sylvilagus nuttallii*) by quantification of the dispersion of a population inhabiting a sagebrush-juniper scabland community in central Oregon.

Within its range, Nuttall's cottontail is reported to occupy ridges and slopes vegetated with sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* sp.), western juniper (*Juniperus occidentalis*), mountain mahogany (*Cercocarpus ledifolius*) at low elevations, upward into pinon pine (*Pinus edulis*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*) zones (Orr, 1940; Janson, 1946; Ingles, 1965). Apparently, plains areas without rocky outcrops or thick brush are not occupied (Orr, 1940). However, to our knowledge, dispersion of a population of Nuttall's cottontails in an area encompassing different vegetative, edaphic, and topographic substrates has not been quantitatively evaluated.

Study Area and Methods

An 84.9-ha study area was established 4.9 km west of Terrebonne, Deschutes County, Oregon, in July 1972, but was shifted about 90 m north (one row of traps) and increased in size to 87.0 ha in April 1973. The area was situated in a sagebrush-juniper scabland community of the Columbia Basin Physiographic Province (Franklin and Dyrness, 1969). From an aerial photograph of the area (Fig. 1) three distinct habitat types were discernible. Habitat Type 1 comprised about 18.2 ha of the study area, and was about 835.4 m in elevation with a flat topography and very fine pumice soils. Habitat Type 2 incorporated about 46.1 ha, ranged in elevation between 835.4 m and 841.5 m,

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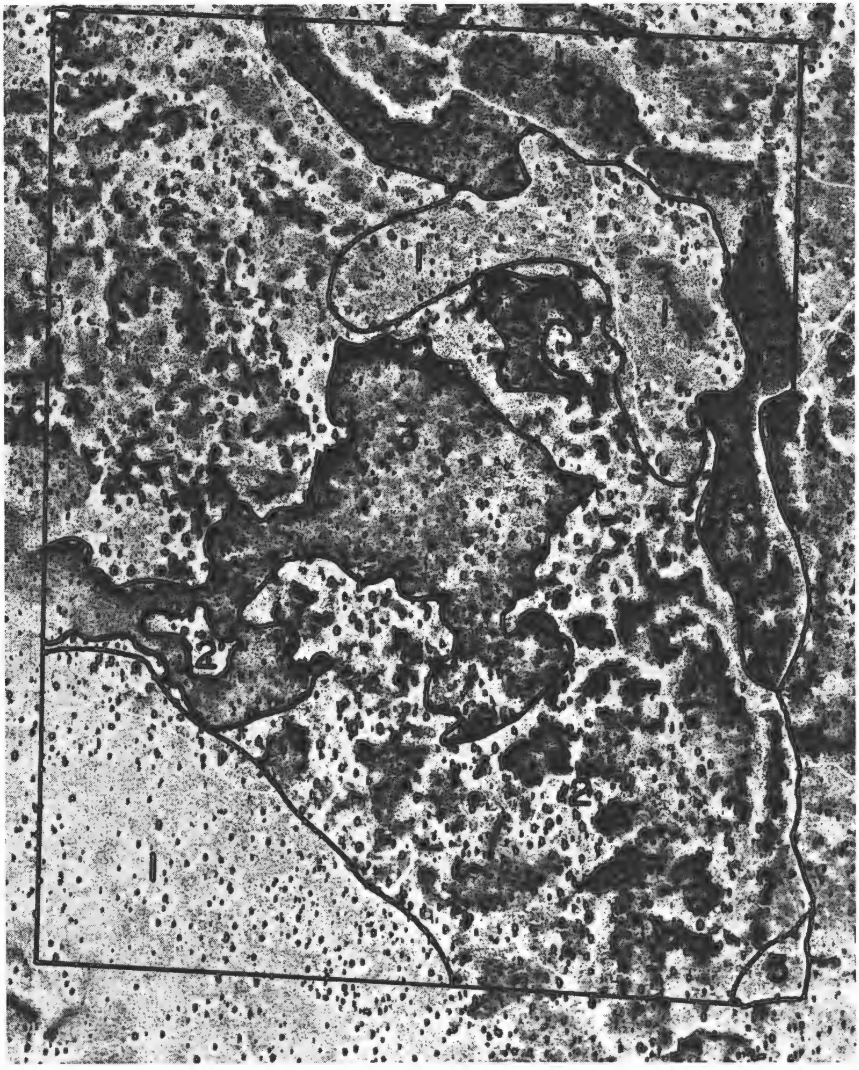

Figure 1. Aerial photograph of the study area with portions in different habitat types delineated and numbered, Deschutes County, Oregon, 1970.

and consisted of a mosaic of small lava hummocks between narrow valleys with deep pumice soils. Habitat Type 3 included about 22.6 ha of broad flat lava hummocks at the 841.5 m elevation with shallow soils that contained numerous pebbles and stones.

During July 1973, the vegetation was sampled by establishing 10 rectangular quadrats (0.3 X 0.6 m) at 10-m intervals along 10 randomly established transects in each habitat type. Species of plants occuring in each quadrat were recorded; percentage fre-

quency of occurrence of species in quadrats was used to evaluate vegetative differences among the habitat types.

Populations of Nuttall's cottontails on the study area were sampled by livetrapping with 15- x 18.7- x 58-cm unbaited cedar box-traps distributed in a 9- x 13-trap grid with approximately 90 m between traps. Livetrapping was conducted for 30 consecutive days during August 1972 and 1973, for three days on alternate weekends during April and May 1973, and for three days each week during June and July 1972 and 1973. Locations of sites of capture within the grid were recorded for each cottontail. During trapping periods in 1973, sites at which cottontails were flushed were recorded; numbered markers were erected at 30.5-m intervals along 32 parallel transect lines 30.5 m apart to facilitate locating the sites at which cottontails were flushed.

Results

Vegetative Survey

Growth of herbaceous species ceased prior to the survey; consequently, plant species recorded on the study area were primarily perennial shrubs, and the dried remains of a few forbs and grasses (Table 1). Cheatgrass, *Bromus tectorum*, the most commonly

TABLE 1. Percent frequency of occurrence of plant species in 100 quadrats established in each habitat type on the study area, Deschutes County, Oregon, July 1973.

Species	Percent Frequency of Occurrence		
	Habitat Type 1	Habitat Type 2	Habitat Type 3
Bromus tectorum[1]	43	75	84
Chrysothamnus viscidiflorus[1]	29	30	5
Sitanion hystrix[1]	23	12	4
Stipa thurberiana[1]	18	32	7
Artemisia tridentata[1]	16	5	13
Eriogonum vimineum[1]	10	1	3
Chrysothamnus nauseosus	2	1	3
Juniperus occidentalis	1	1	2
Sisymbrium altissimum	1	—	—
Mentzelia albicaulis	—	18	—
Agropyron dasystachum	—	6	1
Festuca idahoensis	—	4	4
Purshia tridentata	—	1	2
Agropyron spicatum	—	—	9
Poa sandbergii	—	—	8
Poa cusickii	—	—	4
Leptodactylon pungens	—	—	1

[1]Frequency of occurrence significantly different ($P < 0.01$) from that expected based on uniform occurrence in all habitat types.

encountered plant in all habitat types, occurred almost twice as frequently in quadrats in Habitat Types 2 and 3 as in Habitat Type 1. Three species, green rabbitbrush (*Chrysothamnus viscidiflorus*), squirreltail (*Sitanion hystrix*), and Thurber's needlegrass (*Stipa thurberiana*) appeared to be of major importance in Habitat Types 1 and 2, but of little consequence in Habitat Type 3 (Table 1). Other major differences in vegetation between habitat types were the relatively low species diversity but relatively high percentage frequency of occurrence of most species in Habitat Type 1, and the relatively high species diversity but relatively low percentage frequency of occurrence of many

species in Habitat Type 3 (Table 1). Species diversity and percentage frequency of occurrence of species present were intermediate in Habitat Type 2.

Cottontail Dispersion

During 1972 and 1973, sites for 457 captures of Nuttall's cottontails were recorded. In both years, dispersion of capture sites in relation to habitat type was significantly different ($P<0.05$) from the expected dispersion based on the proportion of each habitat type occurring on the study area (Table 2). Cottontails were captured considerably

TABLE 2. Dispersions of Nuttall's cottontails in relation to habitat based on numbers caught in live traps or flushed in each habitat type on the study area, Deschutes County, Oregon, 1972-1973. Expected numbers based on proportion of study area in each habitat type in parentheses.

Year	Method of Observation	Habitat Type 1	Type 2	Type 3
1972	Livetrapped	84 (65)[1]	168 (153)[1]	38 (72)[1]
1973	Livetrapped	46 (35)[1]	92 (89)[1]	29 (22)[1]
1973	Flushed	11 (18)	46 (46)	29 (22)

[1]Numbers observed significantly different from numbers expected ($P<0.05$).

more frequently than expected in Habitat Type 1 and considerably less frequently than expected in Habitat Type 3. Numbers of captures in Habitat Type 2 did not deviate greatly from expected numbers (Table 2). Because there were no significant differences ($P>0.3$; $X^2=1.529$, d.f.=1) in numbers of captures in the habitat types between years, these data were combined for subsequent analyses.

During 1973, Nuttall's cottontails were flushed at 86 locations. The dispersion of sites at which cottontails were flushed was not significantly different from the expected dispersion based on the proportion of each habitat type occurring on the study area ($0.10>P>0.05$; $X^2=4.759$, d.f.=2). However, 32 percent more cottontails than expected were flushed in Habitat Type 3 and only 61 percent as many as expected were flushed in Habitat Type 1 (Table 2). Dispersion based on records of cottontails flushed was significantly different from that based on livetrapping records ($P<0.05$).

Discussion and Conclusion

We believe that explanation of our observed differences in dispersion lies in a combination of the diel activity patterns of Nuttall's cottontails, and in the physiographic and vegetative differences in habitat types. Because records of cottontails flushed were obtained during periods that livetraps were examined (about 0700 to 1500 PST), we believe that these records were influenced by the diurnal activity of cottontails. Likewise, we believe that dispersion of captures in live traps tended to reflect the nocturnal activities of the species.

Nuttall's cottontails appeared to use crevices and fissures in lava outcrops as daytime retreats, and were commonly observed in or near such formations. They were flushed much less frequently from forms of the type used by eastern cottontails (*S. floridanus*) and some other lagomorphs; apparently, the sparse, mostly shrubby vegetation in the sagebrush-juniper scablands is not conducive to construction and use of forms. Although we did not measure activity systematically, Nuttall's cottontails appeared to begin foraging early in the evening and retired to their daytime retreats early

in the morning. Similar periods of activity were reported for other lagomorphs (Lord, 1961, 1964; Mech *et al.*, 1966).

Habitat Type 1 was essentially devoid of lava outcrops; the paucity of suitable daytime retreats may account for the relatively few cottontails flushed there. The relatively low numbers of Nuttall's cottontails flushed and the larger than expected numbers caught in live traps in Habitat Type 1 tended to indicate that most extensive use of that habitat type occurred during the hours of darkness. We suspect that Nuttall's cottontails foraged in Habitat Type 1, but returned to areas with suitable refuges during the daylight hours. Cottontails may have entered our traps set in Habitat Type 1 to obtain shelter similar to that provided by crevices and fissures in lava outcrops in other habitat types; such behavior could explain, in part, the larger than expected numbers caught in live traps in Habitat Type 1.

We believe that fewer Nuttall's cottontails were present in Habitat Type 3 than indicated by the number flushed in that habitat type. Crevices that appeared to be suitable daytime retreats for Nuttall's cottontails were present in Habitat Type 3, although considerably less abundant than in Habitat Type 2. Consequently, this feature alone doubtfully explains the larger than expected numbers of Nuttall's cottontails flushed in Habitat Type 3. We suspect that the relatively flat topography and the sparse vegetation on the thin stony soil permitted easy visibility of cottontails that were flushed; in turn, these factors caused counts of cottontails flushed in Habitat Type 3 to be elevated. If densities of cottontails were actually lower in Habitat Type 3 as postulated, fewer captures than expected would be a logical assumption. In addition, the low frequency of occurrence of some plant species in Habitat Type 3 that were common in Habitat Types 1 and 2 (Table 1) suggests that those cottontails residing in Habitat Type 3 may have foraged considerably elsewhere, and were not subject to capture in live traps set within this habitat type during much of their period of activity. Habitat Type 2, with an abundance of preferred daytime retreats supplied by innumerable crevices and fissures in low lava hummocks in close proximity to vegetation of a type sought by foraging cottontails, seemingly should be preferred by Nuttall's cotttontails and support more dense populations of them.

We strongly suspect that Habitat Type 2 supported more Nuttall's cottontails and that the observed habitat preferences of the species on our study area were artifacts of the methods of quantification of dispersion of the cottontail population.

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Literature Cited

Franklin, J. F., and C. T. Dyrness. 1969. Vegetation of Oregon and Washington. U.S. Dept. Agr. For. Serv. Res. Paper PNW-80. 216 pp.

Ingles, L. G. 1965. Mammals of the Pacific States: California, Oregon, and Washington. Stanford University Press, Stanford, California. 506 pp.

Janson, R. G. 1946. A Survey of the Native Rabbits of Utah with Reference to Their Classification, Distribution, Life Histories and Ecology. Utah State Agr. Coll., M. S. Thesis. 103 pp.
Lord, R. D., Jr. 1961. Seasonal changes in roadside activity of cottontails. J. Wildlife Manage., 25: 206-209.
————. 1964. Seasonal changes in the activity of penned cottontail rabbits. Anim. Behav., 12: 38-41.
Mech, L. D., K. L. Heezen, and D. B. Siniff. 1966. Onset and cessation of activity in cottontail rabbits and snowshoe hares in relation to sunset and sunrise. Anim. Behav., 14:410-413.
Orr, R. T. 1940. The Rabbits of California. California Acad. Sci. Occas. Papers 19. 227 pp.

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ANNOUNCEMENT

The Northwest Scientific Association and the Editorial Board are pleased to announce that

DONALD R. SATTERLUND

will become

Editor of *Northwest Science*

Effective with the February 1979 issue

Papers and correspondence should be addressed to him at the following address:

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Association News

The annual fall meeting of Officers and Trustees was held in Ellensburg, Washington, on October 28, 1978 with President Ronald Taylor presiding. The agenda included reports from the secretary, treasurer, and editor; it also included a review of plans for the 1979 meeting and reorganization of standing committees. The treasurer reported that the financial status of NWSA needs immediate improvement and he presented a list of recommendations toward that end. Several recommendations that affect members directly were adopted. They are: No issues of Northwest Science will be sent until dues are paid. To be in good standing a member must pay his or her dues by January 15. A late dues charge of $2.00 will be assessed. At least two research grants will be awarded in 1979; however, the total amount to be awarded will be limited to $200. The requirement that at least one author of a paper submitted to NWS also be a member of the Association was adopted at the fall meeting.

President Taylor reviewed plans for the 1979 meeting to be held at Western Washington University on March 29, 30, and 31. The program chairman is Dan Guthrie. Robert Christman is chairman of local arrangements and Gary Lemon is field trip coordination chairman. A symposium entitled "Ecology of Alaskan Arctic Beaches" is being planned.

Section chairpersons are:

Botany	Richard Fonda, WWU
Forestry	Richard Williamson, DNR
Geology	Scott Babcock, WWU
Science Ed. & Math	Willard Brown, WWU
Chemistry & Physics	John Whitmer, WWU
Social Science	James Scott, WWU
Soil and Water	Robert Zasoski, UW
Zoology	Dan Guthrie, WWU

In other business, the size of standing committees was reduced to three members, each serving three-year terms. Adolph Hecht was appointed to serve as chairman of a special committee to examine the records of the Association and to recommend what should be saved and contributed to an archive.

The following appointments have been made by President Taylor:

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